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Tracy Elliot Hazen

Present Evolutionary Tendencies and the Origin of Life Cycles in the Uredinales

By

HERBERT S. JACKSON

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Present evolutionary tendencies and the origin of life cycles in the Uredinales[1]

HERBERT S. JACKSON

Much has been written in an effort to throw light on the problem of the origin of the Uredinales and particularly of the phenomena of heteroecism. Such speculation is always interesting to the mycologist or the student of general phylogeny, and no doubt serves a useful purpose in advancing thought and in stimulating investigation of this important group of plant parasites. It must be admitted in general, however, that the origin of the rusts as a group and the origin of the phenomenon of heteroecism are speculative problems which are as yet unsolved and are very likely to remain so.

It is not the primary purpose at this time to discuss these larger questions. This paper has been prepared, rather, with the idea of attempting to develop, from the evidence available, a logical viewpoint with reference to the present evolutionary tendencies within the group. It would seem that when a clearer conception of the present trend of development is available, it should be possible to discuss with greater understanding the larger question of the origin and relationship of the group as a whole. In connection with this discussion I hope to be able to throw some new light on the problem of the origin of the various types of life cycle which are characteristic of this group of fungi and to establish a basis for a discussion of the relationship between heteroecism and autoecism.

In developing this discussion I shall assume the validity of certain generally acknowledged principles. These will be reviewed briefly in the following paragraphs.

It is evident that the parasitic mode of life must have been acquired at a very early stage in the phylogenetic history of the group. All the rusts known today are obligate parasites and occur only on pteridophytes or spermatophytes. The group is, on the whole, rather sharply distinguished from the other groups of the fungi, the closest probable relatives being found in the Ustilaginales and parasitic Auriculariales.

To a close student of the rusts it is evident that the host has been a very important factor in the evolution of species in this group. As the

[1] Contribution from the Department of Botany, Purdue University Agricultural Experiment Station. Presented in part before the Mycological Section of the International Botanical Congress held at Ithaca, New York, Aug. 1926 (Jackson, 1929).

The writer is greatly indebted to Drs. C. E. Allen, E. M. Gilbert and E. B. Mains for helpful suggestions made during the preparation of this paper and to Drs. J. C. Arthur, H. H. Whetzel, B. O. Dodge, J. H. Faull and F. D. Kern for reading the manuscript.

higher plants have gradually developed during past ages, the rusts parasitic upon them have likewise undergone development. There is much to support this principle. Dietel (1904) has reviewed the evidence in some detail. The extensive development of the autoecious genus *Phragmidium*, confined to the Rosaceae, and particularly that of the group of species occurring on *Rosa*, furnishes an excellent example. The large genus *Ravenelia*, with very few exceptions, is confined to the Leguminosae. Among heteroecious rusts the genus *Gymnosporangium*, including over 50 distinct species, is confined to the Cupresseae in the telial stage and, with two or three exceptions, to the Pomaceae in the aecial stage. Many families of phanerogams especially those having a wide geographical range, often include hosts of a considerable number of rust species, either all evidently related or showing a great diversity in form or life history. Genera or groups of genera in host families which are evidently in an active state of evolution at the present time and which present great difficulties for the spermatophytic taxonomist are often hosts for rusts which reflect this condition and offer similar difficulties to the uredinologist. As examples may be cited the rusts occurring on *Rosa* and *Rubus* in the Rosaceae, and the species of *Puccinia* parasitic on the Violaceae and Cichoriaceae, together with those occurring on *Vernonia*, *Eupatorium*, and *Baccharis* of the Carduaceae.

It is also evident that specialization to host was developed at a comparatively early stage in the evolution of the rusts. While it is quite possible that the very early or ancestral rusts were not highly specialized and that they may have occurred on a wide range of hosts, there is abundant evidence that a high degree of host-specialization had developed at an early period. No other explanation is possible for the remarkable development of related rust species which occur on *Baccharis* or *Vernonia* (Jackson, 1918). Here again the heteroecious genus *Gymnosporangium* is an excellent example. At the present time specialized adaptation to specific hosts appears to be the rule and the lack of it the exception in all forms which have been closely studied. The recently developed knowledge with reference to physiologic forms of *Puccinia graminis Tritici* and of *P. triticina* and others may furnish a clue to the development of species through adaptation to evolving hosts followed by the development of slightly distinct morphological characters.

The interesting and almost unique phenomenon of heteroecism is also considered by many authors to be an ancient character in the group. All the rusts which occur on pteridophytes whose life history is fully known are long-cycled and heteroecious with their aecia on Abieteae. All the rusts

occurring on Abieteae are the aecial stages of heteroecious species with the exception of a very few short-cycled forms which will be discussed later. The fact, then, that the rusts which occur on the pteridophytes and gymnosperms are all heteroecious may be taken for the present as an indication that the phenomenon of heteroecism is an ancient one in this group. This subject will be discussed in more detail after the evidence with reference to the trend of development as between the various types of life cycle has been examined.

RUSTS OF UNSTABLE OR COMPOSITE LIFE HISTORY

The general impression among mycologists and even among some uredinologists, until quite recently, has been that the life cycles in existing species of rusts are quite definitely fixed. A small amount of literature has appeared in recent years which has tended to show that this conception is not altogether true. If one searches for them, it is not at all difficult to find species of rusts which exhibit evidences of being in an unstable condition with reference to life history. The literature bearing on this point will now be reviewed and a number of cases which have come to the attention of the writer from the study of herbarium material will be discussed.

Puccinia Helianthi

Puccinia Helianthi Schw. is a well-known autoecious rust having all spore stages, as has been amply demonstrated by a number of investigators both in this country and abroad. None of the earlier reports of culture work suggested anything unusual about this species. It remained for Carleton (1904) in his study of *P. Helianthi* to note the occasional occurrence of pycnia with the uredinia. Following inoculation in the autumn of *Helianthus petiolaris* and *H. annuus*, with mixed urediniospores and teliospores from *H. petiolaris*, he obtained infection as follows:

> On November 8 there resulted one rust spot on the latter host and three on the former. The spots were of the uredo stage, but the interesting feature accompanying this culture was the appearance first of spermogonia in one of the spots. This fact made it probable that a part of the infection resulted from the teleutospores of the infecting material, even at this unusual season for the germination of these spores.

In another paragraph he says:

> The aecidium occurs rarely in comparison with the occurrence of other stages, but is to be found on a number of hosts and occasionally in considerable abundance. This rarity of its occurrence, together with the occurrence of spermogonia so often with the uredo, may be accounted for by the fact that the uredo is often produced by direct teleutosporic infection.

These are the only references made by Carleton to this phenomenon. Bailey (1923), however, amply demonstrated that *Puccinia Helianthi* on *Helianthus annuus*, while commonly developing aecidia with pycnia from teliosporic infection, very frequently exhibits a phenomenon of 'short-cycling', uredinia instead of aecidia accompanying the pycnia.[2] He says in part:

> The normal development of pycnia and acecia does not always follow teliosporic infection. There is a distinct tendency for the rust to omit the aecia and develop uredinia after the production of pycnia. The uredinia produced by short-cycling subsequent to pycnial formation usually had a very distinct appearance. They developed below pycnia and were confined to definite, light colored, slightly hypertrophied spots. The length of the incubation period also served to distinguish them from ordinary uredinia which usually developed within from five to seven days after inoculation. Short-cycled uredinia, on the other hand, do not develop until two or three days after the pycnia and then are limited to the region directly beneath them. . . . . In our experience, although short-cycling was not frequent, it occurred often enough and was so clear that no doubt remains that it actually does take place.

Puccinia punctata

Wurth (1904, 1905) in his report of culture work with *Puccinia punctata* Link (*P. Galii* Schw.) has shown that at least three physiologic forms of this species (*P. Galii* on *Galium mollugo* and *G. verum; P. Galii-sylvaticae*; *P. asperulae-odorata*) may develop pycnia with aecia or pycnia with uredinia from basidiospore infection. In this connection it is worthy of note that *P. Celakovskyana* Bubák, occurring on *Galium cruciata*, has also been shown by Wurth (1905) to be a brachy-form. There occur, then, on *Galium*, a long-cycled species made up of a number of physiologic races, some of which have been shown to be in a mutable condition between an eu-form and a brachy-form, together with a correlated brachy-form, perhaps best interpreted as a physiologic race of the former, in which the brachy-condition has apparently become fixed.

Puccinia Podophylli

One of the most extensive studies of a rust species which exhibits evidence of being in an unstable condition as to life history was made of *Puccinia Podophylli* Schw. by Whetzel, Jackson, and Mains (1925). This

[2] Throughout this paper the terms aecium, uredinium, and telium and their derivatives will be used in the morphological sense as originally proposed by Arthur (Bot. Gaz. **39**: 219–222. 1905). Since, however, the more recent interpretation of these terms by Arthur (Bot. Gaz. **80**: 219–223. 1925) and Arthur and Kern (Mycologia **18**: 90–93. 1926) would, for example, define a primary uredinium in a brachy-form as an aecium, the writer has occasionally used the terms *aecidium* and *aecidia* in order to avoid any possibility of confusion as to the morphological character of the sorus under discussion.

species is an -opsis form, possessing only aecia and telia in its life history. It is of special interest because teliospores are developed at two different periods during the season. The first crop appears early in the spring on the sheath leaves or bud scales; on the stem, usually at the base; and occasionally on the sepals. The second crop appears later in the summer on the under side of the fully expanded and matured leaves. Between these two crops of teliospores the aecia, usually preceded by pycnia, are developed on the young expanding leaves. Another point of interest in this species is that telia often develop in association with the aecial clusters on the leaves, and to all appearances on the same mycelium, before the appearance of the second crop of teliospores.

As the results of a carefully planned and extensive series of culture experiments it was shown that

> The teliospores of both the early and late crops are functionally and morphologically indistinguishable and the basidiospores developed on the promycelium of either sort may . . . . cause infection on any exposed portion of the *Podophyllum* plant. When infection takes place on the sheath leaves, stems, or sepals, telia are at once produced. They may or may not be accompanied by a few pycnia or aecia. When, on the other hand, infection takes place on the blade of the leaf, pycnia followed by aecia are developed. Aecia may develop without accompanying pycnia. Telia similar to those on sheaths and stems may or may not accompany the aecia on the leaves, and when present develop from the same mycelium as the aecia.

No evidence of repeating aecia was found and no support was obtained for Olive's (1913) hypothesis that perennial haploid and diploid mycelia exist independently in the infected host plants. When mature leaves are infected by basidiospores, telia may predominate over the aecia with or without the production of pycnia. It was suggested that the food conditions of the various tissues invaded have an important influence on the spore form developed. (See Dodge, 1929, pp. 1755, 1763.)

Puccinia Podophylli, according to this study, appears to be in an unstable or plastic condition as to life history and serves to illustrate the sort of changes which may take place in the evolutionary development from a complex to a simpler form of life history. The species is evidently in a transitional condition between an -opsis and a micro-form.

The studies outlined in the preceding pages include some of the most important experimental evidence bearing on the question of mutable species in the rusts. Other similar studies and observations will be referred to in the following pages. In general, however, it may be said that the experimental evidence bearing on this subject is very meager. It happens that few of the species that exhibit any evidence of being in an unstable

condition as to life history have been studied in culture. Many such species, however, exist, and, in connection with taxonomic studies of the rusts made during the past few years, the writer has been on the watch for species which exhibit this tendency and considerable evidence has been obtained from a study of herbarium material.

Puccinia Orbicula

Ten years ago the writer became interested in *Puccinia Orbicula* Peck. This rust occurs on species of *Nabalus* and was originally described as possessing uredinia and telia only. The type specimen shows pycnia with the uredinia, thus indicating that the species should be classed as a brachyform. Aecidia are, however, known to be present in many collections of this species. A careful study was made of the material of *P. Orbicula* in the Arthur Herbarium. It was found that nine collections of primary infection are preserved that show pycnia with uredinia only. There are, however, fourteen collections that show aecidia in greater or less abundance. A careful study of the latter group of collections reveals that all but one show some evidence of a mutable condition. Pycnia occur with aecidia or with uredinia. Uredinia are often associated with the aecidia, and telia are often associated with the primary uredinia. Teliospores are common in the primary uredinial sori even in the type specimen.

This situation is best illustrated by an analysis of the sori occurring on a collection made May 9, 1890 on *Nabalus albus* at Fern, near Greencastle, Ind., by J. C. Arthur. This collection consists of three leaves, and a careful study of the sori under the binocular microscope revealed the following situation:

Leaf A. Infection has resulted in four groups of sori which may be described as follows:

Group 1. Pycnia occur in the center of this group and involve a vein of the leaf. Surrounding the pycnia is a group of six aecidial cups, and immediately associated with these and irregularly surrounding them are eight to ten small sori bearing urediniospores.

Group 2 occurs on a leaf vein. A group of pycnia is surrounded by four aecidial cups with which are associated five uredinial sori that contain some teliospores.

Group 3 occurs at the margin of the leaf near the petiole. The pycnia occur in a group at the edge of the leaf, five aecidial cups surround the pycnia on one side, and closely associated with them is one uredinial sorus in which teliospores are present in abundance.

Group 4 occurs on a petiole. A group of pycnia is associated with a number of uredinia in which teliospores are present. No aecidia occur.

Leaf B. This leaf also shows four groups of sori as follows:

Group 1 occurs on the petiole and shows a number of pycnia with which are associated one aecidial cup and several uredinia in which teliospores predominate.

Group 2 is located in association with one of the main leaf veins near the base, close to the petiole. It consists of a group of pycnia, one aecidial cup, and six or seven uredinia containing many teliospores.

Group 3 occurs on a main vein above group 2, and includes a group of pycnia associated with two unopened aecidia and four uredinia containing many teliospores.

Group 4 is situated on the blade of the leaf, not immediately associated with a vein, and consists of a group of pycnia surrounded by five aecidial cups with no associated uredinia.

Leaf C. This leaf bears eight groups of sori, seven of which occur on the blade of the leaf and one on the petiole.

Groups 1–6 occur on the blade of the leaf and each includes a group of pycnia with uredinia in many of which teliospores are present. No aecidia occur in any of these groups.

Group 7 also occurs on the blade of the leaf and includes pycnia and one aecidial cup with two associated uredinia.

Group 8 occurs on the petiole and consists of pycnia with uredinia in some of which teliospores predominate.

This collection, as noted above, was made early in the season and all the infection is obviously from basidiospores as is indicated by the presence of pycnia in each of the 16 groups of sori. There is no indication of infection from overwintered urediniospores or of secondary infection from aeciospores or urediniospores on any of the leaves.

Another collection of *Puccinia Orbicula* made at Terre Haute, Indiana, May 18, 1893 includes several leaves showing abundant infection with all possible combinations of pycnia, aecidia, uredinia, and telia. None of the leaves show any indication of secondary infection or of infection from overwintered urediniospores. The rust on one of the leaves of this collection was carefully analyzed; 19 groups of sori are present as follows:

4 groups showing 0, I
2 groups showing 0, II
3 groups showing 0, I, II
4 groups showing 0, II, III

3 groups showing 0, I, III
2 groups showing 0, III
1 group showing 0, I, II, III

In nearly all cases in which telia are indicated, the reference is usually to uredinia in which teliospores were more abundant than urediniospores. In these and other collections it is not uncommon to find a tendency, when the infection occurs on the petiole, and to a lesser extent when it occurs on a larger vein, toward the production of pycnia with uredinia or of pycnia with sori in which teliospores predominate. Rarely are aecidia found on petioles. This condition suggests that differences in available food may have an influence on the type of sorus developed from the infection.

It should be noted that in this and in the collection previously discussed, all the primary conditions of an eu-form, a brachy-form, or a micro-form may exist in this species and, what is more important, that all these conditions may exist on the same leaf. *Puccinia Orbicula*, then, exhibits an inherent tendency to an instability in life history, and the observed phenomena suggest the manner by which a brachy-form as well as a micro-form might be derived from an aut-eu-form.

Puccinia effusa

Another species which was studied in some detail was *Puccinia effusa* Diet. & Holw. This is a rather rare form occurring on certain species of *Viola* in the Pacific Coast region of North America. This species is commonly considered an -opsis form, only aecia and telia occurring in the life history, though a few urediniospores are found in the telia in some collections. One collection on *Viola lobata* which was studied in detail may be taken as more or less typical of this species. This collection was made at the type locality near Dunsmuir, California, May 29, 1894 by E. W. D. Holway. The specimen which is preserved in the Arthur Herbarium consists of 17 leaves all of which show some rust. The infection in all cases appears to be primary, from basidiospores. An analysis of the rust on this collection shows a total of 80 groups of sori with the following arrangement:

14 groups showing 0, I
16 groups showing 0, I, III
47 groups showing 0, III
3 groups showing III (no pycnia seen)

In the groups showing O, I, III, the telia occur immediately associated with the aecia, evidently from the same mycelium. In some cases these

telia are ruptured slightly in advance of the aecia. While the associated telia are usually found at the outside of the group of aecia, it is not uncommon to find them intermixed, and occasionally the aecia are outside the telia. Another interesting feature of this and of other collections of this species is the occasional occurrence of teliospores in the aecial cups. In some cases only a few teliospores occur at one side of the cup while in others about half the cup contains chains of aeciospores and the other half teliospores. In other cases it is evident that a few chains of aeciospores occur in sori that are made up in the main of teliospores. In such cases it is apparent that the two sorts of spores arise from the same hymenium. It would appear also that in such mixed sori the peridium is lacking on the side where the teliospores are present.

A similar occurrence of teliospores in aecial cups is not uncommon in certain species. It has been repeatedly noted in the literature and will be mentioned further in connection with a discussion of -opsis forms later in this paper.

When the sori occur on the petioles or at the base of the leaf where the veins of the leaf converge to join the pedicel, there is a strong tendency for the infections to develop only pycnia and telia, though this may occur also on the blade of the leaf. The three cases noted above in which pycnia were not observed with the telia were groups that occurred on the petiole.

Puccinia effusa has not been collected many times, but all the collections made in the spring are evidently of primary infection and all show more or less of this unstable condition. The aeciospores evidently give rise to scattered telia later in the season. There is no evidence of repeating aecidia.

It would appear that this species exhibits evidence of being in an unstable condition between an -opsis type of life history and the micro-type and the observed phenomena are suggestive of the method by which micro-forms might be derived from aut-opsis forms.

In this connection some observations made on *Puccinia Violae* (Schum.) DC. are of interest. This species is an aut-eu-*Puccinia* which is very common in the north temperate regions of both hemispheres. It occurs on a large number of species of *Viola*. While no extensive cultural study of this species has yet been made, it is quite probable that a considerable number of physiological races are present and that these races are specialized to certain host species or groups of species. It is well known, as has been pointed out by Arthur and Holway (1901) and by Holway (1907), that *Puccinia Violae* is a very variable species in its morphology.

At one time or another several species have been proposed based on slight differences.

One of these proposed species was *Puccinia densa* Diet. & Holw., founded on the violet rust as it occurs in the Pacific Coast region on *Viola glabella*. An examination of several collections of this form showing primary infection reveals that telia are commonly associated with the aecia, especially when infection occurs on the petioles. Teliospores are also quite commonly found in the aecial cups. In some cases of infection on the petioles telia predominate over the aecia. Later in the season this form, in common with other forms of *Puccinia Violae*, gives rise to scattered uredinia and telia from aeciospore infection. It would appear that the form on *Viola glabella* exhibits a tendency to a shortening of life cycle in a way which might result in an -opsis form of the type of *Puccinia effusa*.

Many other cases of species which show more or less evidence of being in an unstable condition as to life history undoubtedly occur. A few others will be mentioned later. Sufficient evidence has, however, been presented to establish the general principle that species of rusts exist at the present time which are evidently in an active transitional condition as to life history. For this reason it has seemed desirable to provide a detailed review of a few such species as a necessary background for the discussion which will follow. The existence of such species, and their full significance to a discussion of the problem of phylogeny in the group, have been largely overlooked by previous writers on this subject.

It should be clearly understood, however, that no one has yet observed a species permanently change from one type of life cycle to another. The culture experiments and herbarium observations which have been reviewed show that rusts of composite life cycle do exist. This fact, taken together with the evidence to be obtained from a study of correlated species (see pp. 27 to 37), is strongly indicative of the manner by which closely related rusts of different and apparently fixed life cycle may have arisen one from another.

It will be the purpose in the following pages to obtain from the available evidence suggestions as to the manner by which each type of life cycle may have been derived. Before entering upon this discussion, however, it seems desirable to review certain fundamental considerations which have a general bearing on the problems before us.

CYTOLOGICAL CONSIDERATIONS

Cytological investigations have shown that there are two essential periods in the life cycle of a rust. The first of these is the fusion of two cells of the haploid generation to form the first cell of the diploid phase.

The other essential point involves the union of the paired nuclei in the teliospore and the reduction divisions which follow in the development of the basidium (promycelium). It would not appear to be necessary to review in detail the cytological studies of long-cycled rusts (eu-forms). It may be emphasized, however, that these studies, which have included species in such widely separated genera as *Coleosporium*, *Melampsora*, *Cronartium*, *Phragmidium*, *Tranzschelia*, *Puccinia*, and *Uromyces*, some of which are heteroecious, others autoecious, have all given the same results so far as the essential features of nuclear history are concerned. The basidiospore gives rise to a uninucleate mycelium on which are formed first the pycnia and later the aecia. The primordia of the aecia are made up of uninucleate hyphae. At some stage in the development of the aecia, usually at a definite place, the binucleate condition is initiated by the development of a series or layer of fusion cells. From these fusion cells are developed the chains of aeciospores which are always binucleate. The aeciospores give rise to a binucleate mycelium on which develop urediniospores and teliospores. The former act as repeating spores or diploid conidia, giving rise to one or several generations of binucleate mycelia. The teliospores are at first composed of binucleate cells. The nuclei of each cell fuse at maturity or just before the spores germinate. Germination may take place at once or after a period of rest, according to the habit of the species. On germination a basidium is formed consisting of four cells from each of which a sterigma develops on which a uninucleate basidiospore is borne. The fusion nucleus of each cell of the teliospore passes into the developing basidium, where two successive nuclear divisions occur during which meiosis takes place. Septa are laid down between the resulting nuclei; each nucleus finally passes to a developing basidiospore (sporidium) which is hence uninucleate and may give rise to a new haplont; the process is then repeated. (Arthur, 1929, Chap. IV).

The same type of nuclear life history is found in certain typical -opsis forms such as *Gymnosporangium* and *Gymnoconia*, and presumably in such species of *Puccinia* as *P. claytoniata* (Schw.) Peck. We also find the same thing occurring in typical brachy-forms such as *Frommea* (brachy-*Phragmidium*), *Triphragmium*, etc. To these we may add certain microcyclic forms such as *Chrysomyxa Abietis*, *Gallowaya pinicola*, *Endophyllum Sempervivi*, and *Puccinia Malvacearum*, all of which appear to have this same type of nuclear history except that the diploid thallus is eliminated. In some of them the pycnia may be omitted or are abortive.[3]

[3] It should be mentioned that in several of the forms noted in the preceding paragraphs, including some of the eu-forms, the nuclear phenomena in the developing basidium have not been studied. This phase of the cytological study of rusts has been much neglected.

If we take into consideration the various major types of life cycle, it will be seen that all primary infections, that is, those from basidiospores, are of haploid character regardless of the type of spore which is to appear in the first sorus. This sorus may be aecidioid and bear aecidiospores, uredinioid and bear urediniospores, or telioid and bear teliospores. Aeciospores, urediniospores, and teliospores are diploid, and the change from the haploid to the diploid phase takes place ordinarily with the formation of fusion cells in the primordium of the initial sorus regardless of the type of spore to follow. It is evident, then, that among the various types of life cycle the production of any of the major spore forms—aeciospores, urediniospores, or teliospores—may follow immediately after the formation of fusion cells.

While perhaps not so obvious, it is nevertheless true that the potentiality is genetically present in any given species for the immediate production of any spore form which occurs in the life history, as soon as the change from the haploid to the diploid phase has taken place, since such spore forms are produced sooner or later by mycelia descended from the fusion cells. In accordance with this reasoning it would be expected that, in some cases or under some conditions, teliospores might be produced in aecidial cups, or that they might be borne in separate sori on the same mycelium as that which produces aecidia. Teliospores might likewise be expected to appear in the primary uredinia of brachy-forms. Groups of sori resulting from a single primary infection might include aecidia and uredinia or telia. Primary infections in a species which normally produces aecidia might instead develop primary uredinia or telia. The development of spores or sori in such apparently anomalous situations offers no difficulty so far as the nuclear phenomena are concerned. As soon as the initiation of the diploid phase has taken place, any spore form that follows in the life history may, so far as nuclear conditions are concerned, appear at once. As a matter of fact, nearly all the anomalous conditions mentioned have been encountered in the species of unstable life history already discussed.

From what has been said it should not be inferred that the potentialities mentioned in the preceding paragraph are expressed in all species. The great majority of rusts appear to show no tendency to the development of spore forms out of their usual order. The tendency to an instability in life history such as that exhibited by *Puccinia Helianthi*, *P. Podophylli*, *P. Orbicula*, and *P. effusa* has been noted in relatively few species, principally among aut-eu, -opsis, and brachy-forms.

An examination of the literature dealing with the cytology of rusts

leaves one with the impression that there has been a general tendency on the part of most investigators to accept the type of nuclear history reviewed at the beginning of this section as typical and more or less universal for the group, and to attempt to bring into line with this conception their interpretation of any observations that seemed puzzling. The principle stated in the second preceding paragraph has apparently rarely been recognized. This tendency on the part of many students of the cytology of the rusts has undoubtedly resulted in errors of interpretation. Some of the unusual conditions which have been cited, together with similar cases which will be discussed in the following pages, seem to the writer to indicate that it is the variations from this usual type of life history which furnish some of the most important evidence with reference to the present evolutionary tendencies in the group as well as some of the clearest evidence for a workable interpretation of the origin and relationship of the various types of life cycle.

Cytological studies of micro-forms

Since there will be frequent occasion to refer in the following pages to the results of cytological studies, it seems desirable at this time to review briefly the work which has been done on the micro-forms.

One of the most important considerations is the point of the initiation of the binucleate condition in these forms. Fortunately this phase of the subject has received much study on the part of cytologists. It has long been recognized, as first pointed out by Blackman and Fraser (1906), that the micro-forms fall into two general groups, one in which the vegetative mycelium is prevailingly uninucleate and one in which the mycelium and soral primordium are prevailingly binucleate.

For convenience two tables have been prepared in which the name of the rust species studied is followed by the name of the investigator and the date of publication (see literature cited). In table 1 are included those species which have been found to have the mycelium uninucleate. In only a few of these forms have the exact details of the initiation of the binucleate condition been determined. In all of them, however, except certain forms which are uninucleate throughout, it takes place at some stage in the development of the primordium of the sorus.

In the second group (table 2) are listed those species in which the mycelium is prevailingly binucleate. In some of these a small amount of uninucleate mycelium has been noted, but in all of them the primordium of the sorus is binucleate and the change from a uninucleate to a binucleate condition is assumed to take place somewhere in the mycelium. In a

TABLE 1

Microcyclic species with mycelium prevailingly uninucleate

RUST	INVESTIGATOR
*Puccinia Liliacearum Duby	Sappin-Trouffy (1896) Maire (1902)
Puccinia Buxi DC.	Sappin Trouffy (1896) Mme. Moreau (1914)
Puccinia Malvacearum Bertero	Blackman and Fraser (1906) Olive (1911a)† Werth and Ludwigs (1912) Mme. Moreau (1914) Lindfors (1924)
Uromyces Ficariae Lev.	Sappin-Trouffy (1896) Blackman and Fraser (1906) Mme. Moreau (1914)
*Puccinia transformans Ell. & Ev. (error for P. elegans)	Olive (1908)
Puccinia Asteris Duby	Olive (1911a) Walker (1928)
Uromyces Rudbeckiae Diet. & Holw.	Olive (1911a) Jackson (this paper)
*Uromyces scutellatus (Schrank) Lev.	Kursanov (1922)
*Uromyces laevis Koern.	Kursanov (1922)
*Puccinia Rossiana Lagerh.	Kursanov (1922)
Chrysomyxa Abietis (Wallr.) Unger	Kursanov (1922) Lindfors (1924)
*Tranzschelia fusca (Pers.) Diet.	Sappin-Trouffy (1896) Dowson (1913) Lindfors (1924) Walker (1928)
Puccinia Morthieri Koern.	Lindfors (1924)
*Puccinia Cryptotaeniae Peck.	Walker (1928)
Puccinia Xanthii Schw.	Walker (1928)†
*Kunkelia nitens (Schw.) Arth.	Kunkel (1913, 1914) Dodge (1923, 1924) Dodge and Gaiser (1926)
Gallowaya pinicola (Gall.) Arth.	Dodge (1925)
*Endophyllum Euphorbiae-sylvaticae (DC.) Wint.	Sappin-Trouffy (1896) Moreau (1918a, 1919)
Endophyllum uninucleatum Moreau	Mme. Moreau (1912, 1914, 1915) Moreau (1918a, 1919)
*Endophyllum Sempervivi (Alb. & Schw.) DeBary	Maire (1900) Hoffman (1911) Moreau (1918b)
*Endophyllum Valerianae-tuberosae R. Maire	Maire (1900) Poirault (1915)
*Endophyllum Centranthi-rubri Poir.	Poirault (1913, 1915)

* Species in which pycnia have been observed to accompany the telia are designated with the asterisk.

† The paper by Olive (1911a) is a very brief abstract of one which he read before the Botanical Society of America at the Minneapolis meeting (December, 1910) of the A.A.A.S. The full paper was never published. A manuscript copy of the brief paper as ready by Olive has been available to the writer and in addition to his mention of *P. Asteris*, *P. Malvacearum*, and *Uromyces Rudbeckiae* he comments as follows on other species not cited in the published abstract: "In four species, *P. Silphii*, *P. Xanthii*, *P. Heucherae* and *P. Circaeae*, the binucleated cells go back to some indefinite point in the vegetative mycelium. In no case which I have observed, however, does this

TABLE 2

Microcyclic species with mycelium prevailingly binucleate

RUST	INVESTIGATOR
Puccinia Adoxae Hedw. f.	Blackman and Fraser (1906)
Uromyces Scillarum (Grev.) Wint.	Blackman and Fraser (1906) Mme. Moreau (1914)
Botryorhiza Hippocrateae Wh. & O.	Olive (1918)
Puccinia Asarina Kunze	Kursanov (1922)
Puccinia Aegopodii (Schum.) Mart.	Kursanov (1922)
Puccinia Fergusonii B. & Br.	Kursanov (1922)
Puccinia conferta D. & H.	Kursanov (1922)
Uromyces Ficariae Lev.	Kursanov (1922)
Uromyces Gageae G. Beck	Kursanov (1922)
Puccinia Arenariae (Schum.) Wint.	Lindfors (1924)
Puccinia albulensis Magn.	Lindfors (1924)
Puccinia Epilobii DC.	Lindfors (1924)
Puccinia gigantea Karst.	Lindfors (1924)
*Puccinia Holboellii (Hornem.) Rostr.	Lindfors (1924)
Puccinia Saxifragae Schlecht.	Lindfors (1924)
Uromyces Solidaginis (Sommerf.) Niessl.	Lindfors (1924)
Puccinia Hydrophylli Peck & Clint.	Jackson (this paper)

considerable number of the species listed no uninucleate mycelium has been observed.

To the list of published records in table 2 is added *Puccinia Hydrophylli*. This species has been studied in a preliminary way by the writer during the past year. Ample material showing young and mature infections was collected in May, 1927 at Madison, Wisconsin, on *Hydrophyllum virginianum*. This rust is a strict micro-form so far as observed. Only one generation of teliospores develops during a season, and these spores apparently hibernate through the following summer and winter before germinating. Material for cytological examination was fixed in Flemming's medium and in formalin-acetic-alcohol fixatives and stained with Flemming's triple stain and with Heidenhain's iron-alum-haematoxylin. The mycelium appears to be binucleate as far back as it could be traced and in the youngest infections available. No evidence of fusion cells was found. Furthermore, no evidence was found of the presence of a fusion nucleus, even in the most mature teliospores. Pycnia are unknown in this species.

It will be observed that the number of species in the two groups (exclusive of *Endophyllum*) is approximately equal. While it is possible to group

sporophytic condition seem to be pushed back as far as Blackman's *P. Adoxae* and *Uromyces Scillarum;* for in all these forms, mycelium with uninucleated cells may also be found, at even quite an advanced stage of development."

Pycnia are unknown in all these species, and they might be added to the list (table 2), which follows, of forms in which the mycelium is prevailingly binucleate. It should be noted, however, that Miss Walker's (1928) observations on *P. Xanthii* do not fully agree with those of Olive.

them in this manner, a detailed study of the recorded observations, taken as a whole, indicates that, while the initiation of the binucleate condition in some forms occurs in a very definite manner and position in the primordium of the sorus, quite comparable to what takes place in aecidia, in others the transition takes place more or less sporadically throughout the soral primordium. In many forms of the first group the exact position of the fusion cells has not been determined. In the species of the second group the relative proportion of uninucleate to binucleate mycelium varies considerably. In a number of these no uninucleate mycelium has been observed. Taken as a whole, then, the short-cycled forms exhibit considerable variation in this regard.

Those species in which pycnia have been observed to accompany the telia have been marked with an *. It will be noted that a considerable number (about half) of the species included in the first group possess pycnia while pycnia have been recorded in only one species listed in the second group. It is perhaps to be expected that pycnia should not be uncommon in the first group, in which the mycelium is uninucleate, since pycnia are found only on haploid mycelia. The more important point to observe is that they are absent in so many species of the first group. Some of the species possessing pycnia, notably *Uromyces scutellatus*, *U. laevis*, and *Tranzschelia fusca*, are among those whose general development corresponds so remarkably to that of aecidia.

The occurrence of pycnia in *Puccinia Holboellii* listed among those which have binucleate mycelium requires explanation. An examination of herbarium material of this species on a large number of hosts shows that pycnia are not always formed. Lindfors studied this rust on *Erysimum hieraciifolium*. It is evident that no pycnia occurred on his material, since he does not mention them and since he includes the species among those in which he found only binucleate mycelium. It would be especially interesting to have a comparative study made of the nuclear phenomena in this species based on a study of the rust on different hosts, including collections with and without pycnia. If Lindfors' account is correct for the material which he studied, it is to be expected that forms with pycnia would show variations from his observations.

It is well known that pycnia occur sporadically in some species, particularly in microcyclic forms. DeBary (1866, p. 169) observed a case in *Endophyllum Sempervivi*, a species which usually forms pycnia, in which no pycnia were ever developed. He apparently made observations on these plants in culture through several seasons. Miss Walker (1928) says that pycnia were rare in the material of *Puccinia Cryptotaeniae* which she

studied, yet they are known to be abundant in some collections. I have noted in *P. Grindeliae* Peck that pycnia are common in some collections, particularly on certain hosts, and are entirely absent in others. Pycnia were unrecorded for *Gallowaya pinicola* until Dodge (1925) called attention to abortive pycnia in connection with his cytological study of that species.

That pycnia are commonly omitted in microcyclic forms is well brought out in the lists of forms which have been studied cytologically. As a matter of fact, pycnia have been recorded for only 16 of the 148 North American species of micro-*Puccinia* and are produced only sporadically in several of these.

It will be noted from the above tabulation that, with few exceptions, the cytological observations on micro-forms have been made on any given species by only one investigator and usually from material collected on one host and from one locality. For an adequate knowledge of the micro-forms, comparative studies of the same species collected on different hosts, and on the same host from widely separated localities must ultimately be made. *Puccinia Holboellii* would be an excellent species for such a study, since it has a wide range of hosts and a distribution covering both hemispheres. It is further of extreme interest since it is closely correlated with the heteroecious eu-form *P. monoica* and occurs on several of the same hosts as the aecia of the latter species. Another species which gives promise of interesting results in this connection is *Puccinia Grindeliae*. Both species will be discussed in detail later in this paper.

In this connection the results of cytological studies of *Uromyces Ficariae* are of special interest. While this species is recorded on but one host, *Ficaria verna*, it has been examined by a number of workers in widely separated localities. It will be noted that this species has been included in both lists. Sappin-Trouffy (1896) describes the hyphaeas being binucleate. Blackman and Fraser(1906), who reinvestigated this form, report that

> the general mycelium appears to exhibit single nuclei, but the mass of mycelial hyphae round about the teleutospore sorus, as well as those directly connected with teleutospore formation appear to have conjugate nuclei. Thus the haustorium in a host-cell close to the teleutospore mass shows clearly two nuclei.

Mme. Moreau (1914) found the mycelium to be uninucleate, the binucleate phase beginning at the lower cells of the sporiferous plexus of hyphae in the sorus initial. Kursanov (1922)[4] on the other hand found the

[4] Because of the greater availability, the French article by Kursanov published in 1922 has been cited throughout this paper. It should be mentioned, however, that apparently all the original work, together with an amplification of the discussion and a review of the literature, was included in a paper of similar title in the Russian language published at Moscow in 1915.

mycelium to be prevailingly binucleate. He did, however, observe some uninucleate mycelium. These results strongly suggest that there is some variation in this species in different localities. This species is also of special interest since it is one of those micro-forms in which urediniospores are formed in the telial sori. These resemble the urediniospores of *Uromyces Rumicis* (Schum.) Wint., a heter-eu-form which has aecia on the same host. The micro-form and the heter-eu-form are correlated and the former occurs on the aecial host of the latter.

The situation in *Puccinia Arenariae* as described by Lindfors (1924) is of special interest. This species is not known to form pycnia. He studied it on *Melandrium rubrum* and *Arenaria serpillifolium*. With reference to the nuclear condition in the mycelium and the sorus initial he says:

> An investigation of young fundaments of sori, for the purpose of studying the eventual transition of the mycelium cells from uni- to binuclear, gave a negative result. It was seen, however, that all the cells in the sorus fundament, which were hit by the section so that the number of nuclei could be determined contained two, exceptionally several nuclei. No fusion of cells, i.e., migration of nuclei, takes place in this fungus. The binuclear character must have originated in an earlier period. A very careful test of the conditions in the purely vegetative mycelium showed that this also consisted of binuclear cells so far as it was possible to follow it. (Translation)

The two nuclei fuse in the teliospore in the usual way. During the following season he studied the germination of the spores and found that the fusion nucleus passes into the promycelium, where it divides, this division being followed by the formation of a cross wall between the daughter nuclei. These nuclei divide again, but no cross walls were observed to be formed. The basidium is two-celled, each cell having two nuclei, and the two nuclei appear to pass into the basidiospore from each cell of the basidium. In the mature basidiospore two nuclei are constantly present. It would appear from this study that the binucleate condition in the forms of this species studied by Lindfors is initiated by the failure to form cross walls in the basidium after the second nuclear division.

As Lindfors has pointed out, Grove (1913a) has figured a four-celled basidium in this species on *Lychnis diurna* and on *Arenaria trinervis*. I have attempted to verify these observations from a study of herbarium material but without success. It has been possible, however, to demonstrate to my own satisfaction that a two-celled basidium occurs in American collections of this species on *Dianthus barbatus*. Herbarium material is not ordinarily satisfactory for a study of rust basidia unless the material has been very quickly dried. It should be an easy matter, however, to study the gross features of the basidium in fresh material, since this species

commonly shows a lepto-condition. As Grove pointed out, the species is a variable one and presumably includes a number of physiologic forms. This supposition has been confirmed by Wille (1915) who has studied this species in culture.[5] It is not unlikely that forms occur differing in their nuclear history and in the number of cells constituting the basidium.

One of the most interesting species among the micro-forms of *Uromyces* or *Puccinia* is *Uromyces Rudbeckiae*. The only published statement with reference to the nuclear condition in this form is that included in the abstract of Olive (1911a), who says that

> *Uromyces Rudbeckiae* was found to present an enigmatical variation, in that all the cells, teleutospores as well as vegetative mycelium, were discovered to possess each but one nucleus. No explanation can be offered at present for this unique phenomenon.[6]

In the summer of 1927 the writer collected this species on *Rudbeckia laciniata* in the vicinity of Lafayette, Indiana. Material was fixed in Flemming's weak and in formalin-acetic-alcohol fixatives and stained with Flemming's triple stain and with Heidenhain's iron-alum-haematoxylin. This material included the very youngest infections that could be observed, as well as all stages in the development of the sori including those in which the teliospores were germinating. It was possible to confirm in every detail Olive's observations on the nuclear phenomena in this species. Furthermore the germination of the teliospores, as they occurred on the living plant and in fixed material, was studied, and it was determined that this species, in common with *Puccinia Arenariae*, germinates by the development of a two-celled basidium. The nucleus of the teliospore passes into the basidium and divides once. A cross wall is laid down, and from each cell so formed a sterigma develops and the

[5] Though Wille studied this species from a number of hosts and tested the germination of the spores on slides, he does not comment on the character of the basidium.

[6] In the manuscript referred to previously (note, p. 18) Olive elaborates this statement as follows: "One of the most enigmatical variations met with in these studies is seen in the Lepto-form *Uromyces Rudbeckiae* Arthur & Holway on *Rudbeckia laciniata*. All the teleutospores, both young and old; all the stalk cells, in fact, every cell of the whole sorus as well as of the vegetative mycelium so far as it could be traced contain each but one nucleus. I am not yet prepared to affirm the utter absence of the binucleate condition in this rust; but a careful search through young and old stages has so far failed to reveal any such binucleated cells. We can only wildly speculate at present on the significance of such a peculiar condition. A well-defined appearance of synapsis in the mature teleutospores suggests the beginnings of reduction, although I am uncertain whether the promycelium bears just four spores or not. If this appearance proves to be a true synapsis, then that fact would preclude the idea that the teleutospores in this species are gametophytic spores, a phenomenon which would be absolutely unique among the rusts if it were ture, which do not believe.

"The only other alternative is that we have in *Uromyces Rudbeckiae* an early fusion of the sexual nuclei, possibly shortly after the sexual cell fusions. Hence the absence of the paired, conjugate condition, which we have come to regard as universally present in rust sporophytes."

contents of the cell pass through this into the developing basidiospore which is uninucleate. There can be little question that this species is uninucleate throughout.

Uninucleate forms among short-cycled rusts have been noted otherwise only in the endo-forms. Mme. Moreau (1912), shortly after Olive's abstract appeared, published a description of a uninucleate *Aecidium* which she later (1914, 1915) refers to *Endophyllum Euphorbiae-sylvaticae* as a variety, *uninucleatum*. (See also Mme. Moreau 1914, 1915). Poirault (1913, 1915) shows that *Endophyllum Centranthi-rubri* is uninucleate throughout and that the spores germinate with a two-celled promycelium. Kursanov (1922, 1923) has described uninucleate forms in *Aecidium punctatum* Pers. (the aecial stage of *Tranzschelia punctata* (Pers.) Arth. and in *Aecidium leucospermum* DC. (the aecial stage of *Ochropsora Sorbi* Diet.). Attempts to infect the host of the latter, *Anemone ranunculoides*, gave negative results. Soppitt (1893) has, however, shown by means of culture experiments, that this *Aecidium* is capable of repeating itself on the aecial host. In spite of Kursanov's report that the spores germinate with normal germ tubes, the evidence is strong that repeating endo-forms exist in these two species. Finally, Dodge (1924) and Dodge and Gaiser (1926) report uninucleate forms, the spores of which germinate with a two-celled basidium in *Kunkelia nitens*, the caeomoid endo-form related to *Gymnoconia interstitialis* (Schlect.) Lagerh. While the nuclear phenomena are unknown, it is of interest that Olive and Whetzel (1917) report the occurrence of two-called basidia in *Endophyllum Stachytarphetae* (P. Henn.) Wh. & O. and *E. circumscriptum* (Schw.) Wh. & O. Gäumann (1922) figures and describes one- and two-celled basidia in *Puccinia tjibodensis* Gäum. He also figures and records the occasional development of two-celled basidia in *Endophyllum Ixorae* Gäum. The writer has recently observed that the teliospores of *Puccinia Anemones-virginianae* Schw. collected near Toronto, Ontario, on *Anemone virginiana*, germinate with a two-celled promycelium.

The European species of *Endophyllum* have been extensively studied from a cytological viewpoint. The results have been admirably summarized by the Moreaus (1919) and more recently by Dodge and Gaiser (1926). It would seem unnecessary to review this work in any detail at this time. It is desirable, however, to point out the variation in the nuclear phenomena of different species or forms which this work reveals. Reference has already been made to the uninucleate form of *E. Euphorbiae-sylvaticae* and to the uninucleate condition in *E. Centranthi-rubri*. In the more common form of the former species it has been demonstrated quite con-

clusively by Sappin-Trouffy (1896) and more recently by the Moreaus (1918a, 1919) that there is no fusion of the two nuclei in the spore; the nuclei pass into the basidium without fusing and each divides once, the result being a four-celled basidium and uninucleate basidiospores.

Dodge has recently (1929, p. 1758) presented evidence which is suggestive that the nuclei of the uninucleate form of *Endophyllum Euphorbiae-sylvaticae* are diploid. This variety is the only uninucleate form so far discovered in which the spores germinate with a four-celled promycelium.

In *E. Sempervivi* (Hoffman, 1911; Moreau, 1918b, 1919), on the other hand, the conjugate nuclei fuse in the mature spore and the fusion nucleus passes into the basidium where it divides. A cross wall is laid down between the daughter nuclei which then divide again, the result being a four-celled basidium and uninucleate basidiospores.

In *E. Valerianae-tuberosae*, a still different condition is reported by Maire (1900, 1902). According to his results, the young spore has two nuclei but the mature spore has only one, in consequence of the degeneration of one of the two. On germination this nucleus passes into the end of the basidium and is isolated by a cross wall. It then divides once and a cross wall is laid down between the daughter nuclei. According to Maire only the terminal cell produces a basidiospore, the nucleus of the other cell degenerating. Maire reports that he found no pycnia in this species, though they are described by Sydow (1915).

It is worthy of note that only one of the several species of *Endophyllum* which have been examined cytologically exhibits a nuclear history comparable to that of the eu-forms, and that all the others differ from each other in this respect with the exception of the three uninucleate forms.

The situation in *Kunkelia nitens* as revealed by the recent detailed studies of Dodge (1924) and Dodge and Gaiser (1926) is of special interest. Kunkel (1914) had described the nuclear phenomena in this species as occurring in a manner essentially similar to those in *E. Sempervivi* as outlined above. Dodge and Gaiser, however, have shown that in one form of *Kunkelia nitens* there is no nuclear fusion in the spore. Both conjugate nuclei pass into the basidium where each divides once, and a four-celled basidium is formed. This story is essentially that given for *E. Euphorbiae-silvaticae*. Two races of *Kunkelia nitens* which develop fusion cells and four-celled basidia are recognized which seem to differ from one another in the size, color, and form of their spores. Both these races develop pycnia, but in one the pycnia are more numerous and more prominent than in the other. A uninucleate form germinating with a two-celled basidium

is described which develops no pycnia. Another less common form is like the last-mentioned except that pycnia are developed.

The study of *Botryorhiza Hippocrateae* made by Olive (1918) is of interest in this connection. This species occurs on *Hippocratea volubilis* in Cuba and Porto Rico. Its relationship is obscure but quite certainly not with *Endophyllum*. Superficially it might be taken for a lepto-*Uromyces*, but it is perhaps best interpreted as a special type of microcyclic form representing an end product of a line of regressive development in a group that cannot now be recognized (see p. 79). The mycelium is binucleate so far as observed. The conjugate nuclei fuse in the stalked, thin-walled, one-celled teliospores. The basidium is developed apparently in the usual way, with four cells, each of which develops a sterigma on which the uninucleate basidiospores are formed. No fusion cells were observed, and the initiation of the binucleate phase is assumed to take place early in the development of the mycelium. No pycnia are known for this species.

It is unfortunate that the emphasis of the cytological study of microforms in *Uromyces* and *Puccinia* has been almost exclusively directed to a consideration of the initiation of the binucleate phase in the primordium of the sorus and to a search for fusion cells. Very little attention has been given to the accurate determination of whether or not the two nuclei fuse in the teliospore or to a study of the nuclear history in connection with the development of the basidium. The variation shown in these features in the relatively few species of the endo-forms which have been studied suggests that similar conditions will be found in the microforms of *Puccinia* and *Uromyces*. This suggestion is supported by the results obtained with the three species which have been examined.

Puccinia Malvacearum has been examined by a number of workers, including Werth and Ludwigs (1912) and Mme. Moreau (1914). The mycelium is uninucleate, fusion cells occur initiating the binucleate condition, and the conjugate nuclei fuse in the mature teliospore. The fusion nucleus passes into the developing basidium where two successive divisions occur, leading to the formation of a four-celled basidium and uninucleate basidiospores. This procedure is essentially like that in *Endophyllum Sempervivi* and in the eu-forms which have been investigated. It is of interest that we find the same nuclear history in two short-cycled forms of different morphological type, one of which develops pycnia while the other does not. The situation in *Puccinia Arenariae* as described by Lindfors (1924) has already been reviewed as well as my own study of *U. Rudbeckiae*. Three distinctive types of nuclear history are found in the three species which have so far been studied. Gäumann's (1922) report

of one- and two-celled basidia in *Puccinia tjibodensis* is of interest in this connection, though the nuclear phenomena are unknown.

It is unfortunate that *Puccinia Malvacearum* was the first micro-form in this group selected for examination as to the nuclear phenomena of germination. Because the result of this study showed a nuclear condition exactly comparable to that in all the long-cycled rusts which had been examined, there has apparently been a tendency to the assumption that this species was typical for the micro-forms of *Puccinia* and *Uromyces*. This assumption may account for the small number of species which have been studied.

While the study of the nuclear history of germination in those micro-forms of *Puccinia* and *Uromyces* which produce but one generation of teliospores will be difficult, since the spores germinate only after a prolonged resting period, there are a considerable number of lepto-forms, those which germinate at once and develop several generations in a season, which would be relatively easy to study in this particular. Any species would be worth investigating, as confirmation is needed of the studies already made and we need to know whether any given species shows variation in its nuclear behavior in different regions and on different hosts. The host species used in the study is of special importance.

While much more study is needed of the nuclear behavior in short-cycled rusts, the work which has already been done and which has been reviewed above is sufficient to establish beyond doubt that great variation occurs in different species of this group not only with reference to the initiation of the binucleate condition but also with reference to the occurrence or non-occurrence of nuclear fusion, and to the nuclear history in the development of the basidium.

The occurrence of the uninucleate race in *Endophyllum Euphorbiae-sylvaticae*, the report by Lindfors of a binucleate mycelium in *Puccinia Holboellii*, a species which sometimes develops pycnia, and more especially the report by Dodge and Gaiser of the four different types of *Kunkelia nitens*, establish beyond question that forms occur in the same species which differ markedly in their nuclear history. Any attempt at an explanation of the significance of such variations will be reserved for a later part of this paper.

THE PHENOMENA OF CORRELATION

One of the most outstanding features of the rusts is the existence of various types of life cycle. When all the spore stages of a given species are known it is possible in general to refer it to one of the several types of

life history commonly referred to as eu-, -opsis, brachy- or micro-forms based on the subgenera of Schroeter. While, as has already been shown, certain species exhibit a composite or unstable life history, it is nevertheless true that the great majority of rust species, when the full life cycle is known, can be quite accurately assigned to one or another type of life cycle.

It is well known that certain rusts of similar or of different life histories occurring on related hosts show a close resemblance in morphological characters. The term 'correlation' has recently come into rather general use to express this relationship.

Correlation between species of Uromyces and Puccinia

Correlation between species of rusts may manifest itself in various ways. Perhaps the most familiar type is illustrated by the close resemblance which exists between certain long-cycled species of *Puccinia* and of *Uromyces*. In such a case the aecia, uredinia, and telia of long-cycled species (one representing each genus) resemble each other very closely or may even be exactly alike morphologically, the only difference being that the teliospores are in one case two-celled and in the other one-celled. The hosts are usually the same or very closely related species. In many cases the geographical range of the two parasites is the same or one species overlaps the other. When the rusts in question are heteroecious, the aecial hosts are the same or closely related, as are also the uredinial and telial hosts.

Orton (1912) has reviewed this type of correlation and lists among others the following pairs of species:

HETEROECIOUS SPECIES

Puccinia subnitens Diet.—Uromyces Peckianus Farl.
Puccinia extensicola Plow.—Uromyces pedatus (Schw.) Shel.
Puccinia Distichlidis E. & E.—Uromyces acuminatus Arth.
Puccinia Pamellii (Trel.) Arth.—Uromyces graminicola Burr.
Puccinia Eleocharidis Arth.—Uromyces Eleocharidis Arth.
Puccinia angustatoides Stone—Uromyces Rhynchosporae Ell.

AUTOECIOUS SPECIES

Puccinia Epilobii-tetragoni Pers.—Uromyces plumbarius Peck.
Puccinia Gentianae (Str.) Link.—Uromyces speciosus Holw.
Puccinia Ruelliae-Bourgaei Diet. & Holw.—Uromyces Ruelliae Holw.
Puccinia opaca Diet. & Holw.—Uromyces cucullatus Syd.

TABLE 3

Correlation between heteroecious eu- and micro-forms

HETER-EU-FORMS	MICRO-FORMS
Melampsora Abietis-canadensis (Farl.) Ludwig I on *Tsuga canadensis* II, III, on *Populus*	Melampsora (Necium) Farlowii (Arth.) Davis III on *Tsuga canadensis*
Coleosporium sp. I on *Pinus* II, III on various hosts	(Coleosporium) Gallowaya pinicola Arth. III on *Pinus virginiana*
Chrysomyxa (Melampsoropsis) sp. I on *Picea* II, III on Ericaceae	Chrysomyxa Abietis (Wallr.) Unger Chryxomyxa Weirii Jackson III on *Picea* sp.
Puccinia coronata Corda I on *Rhamnus* II, III on *Avena* & other grasses	Puccinia Mesneriana Thuem. III on *Rahmnus*
Puccinia Grossulariae (Pers.) Lag. I on *Ribes* II, III on *Carex*	Puccinia Parkerae Diet.& Holw. III on *Ribes*
Puccinia Polygoni-vivipari H. Dietr. I on *Ligusticum* II, III on *Polygonum*	Puccinia Ligustici Ell. & Ev. III on *Ligusticum* sp. etc.
Puccinia Andropogonis Schw. I on *Penstemon, Comandra, Dasystoma*, etc. II, III on *Andropogon*	Puccinia Pentstemonis Peck III on *Penstemon* Puccinia Seymeriae Burr. III on *Dasystoma* etc. Puccinia Comandrae Peck III on *Comandra*
Puccinia Distichlidis Ell. & Ev. I on *Steironema* etc. II, III on *Spartina*	Puccinia Dayi Clinton III on *Steironema*
Puccinia abundans (Peck) Jackson I on *Symphoricarpos* II, III on *Festuca* etc.	Puccinia Symphoricarpi Hark. III on *Symphoricarpos*
Puccinia canaliculata (Schw.) Arth. I on *Xanthium* and *Ambrosia* II, III on *Cyperus*	Puccinia Xanthii Schw. III on *Xanthium* and *Ambrosia*
Puccinia Asterum (Schw.) Kern I on *Aster* II, III on *Carex*	Puccinia Asteris Duby III on *Aster*
Puccinia universalis Arth. I on *Artemisia* II, III on *Carex*	Puccinia conferta Diet. & Holw. III on *Artemisia*
Puccinia Pattersoniana Arth. I on *Brodiaea* II, III on *Agropyron* etc.	Puccinia Moreniana Dudley & Thomp. III on *Brodiaea*
Uromyces perigynius Halst. I on *Aster, Solidago, Rudbeckia* etc. II, III on *Carex*	Uromyces Solidaginis (Somm.) Niessl. III on *Solidago* Uromyces Rudbeckiae Arth. & Holw. III on *Rudbeckia*
Uromyces Rumicis (Schum.) Wint. I on *Ficaria* II, III on *Rumex*	Uromyces Ficariae (Schum.) Lev. III on *Ficaria*

Correlation between heter-eu- and micro-forms

Another type of correlation is illustrated by the close morphological resemblance between the telia of micro-forms and those of long-cycled heteroecious species. In such a case the long-cycled species bears its aecia on the same host that bears the telia of the corresponding short-cycled rust. Dietel (1897) was the first to call attention to this sort of relationship, when he pointed out the resemblance between the micro-*Puccinia Mesneriana* Thuem., which occurs on *Rhamnus*, and the heter-eu- *Puccinia coronata* Corda, which develops its aecia on *Rhamnus* and its uredinia and telia on grasses. A large number of examples of this type of correlation have been recorded by various authors (Fischer, 1898; Travelbee, 1915; Dietel, 1918; and Arthur and Jackson, 1922). While the larger number have been recorded between species of *Puccinia* and of *Uromyces*, a considerable number of similar cases occur in other genera of the rusts. Table 3 furnishes a partial list only and is inserted here to illustrate the general principle and to serve as a record of some of the species which will be discussed in this paper. This subject will be mentioned again in some detail in connection with a discussion of the origin of short-cycled forms. Other cases not listed here will also be cited.

Examples of correlation between other types of life history might be cited, as, for example, between heter-eu- and -opsis forms, -opsis and micro-forms, and aut-eu- and brachy-forms. There will be occasion to cite specific examples illustrating these various types of correlation in the following pages. It will perhaps be sufficient, for the present, to illustrate this principle by citing the series of correlations which exist between species of *Puccinia* on Onagraceae, which were pointed out by Bisby (1916). The following species of rusts of different life history existing on hosts of that family show very remarkable correlation:

Puccinia Veratri DC. I on *Epilobium* II, III on *Veratrum*	heter-eu-form.
Puccinia Epilobii-tetragoni (DC.) Wint. I, II, III on *Epilobium*, etc.	aut-eu-form.
Puccinia Epilobii-Fleischeri Ed. Fisch. I, III on *Epilobium*	-opsis form.
Puccinia Epilobii DC. III on *Epilobium*	micro-form.

That this is not an isolated case is shown by the following similar series among the rusts occurring on members of the Ranunculaceae:

Tranzschelia punctata (Pers.) Arth.	heter-eu-form.
I, on *Anemone* etc.	
II, III on *Amygdalaceae*	
Tranzschelia cohaesa (Long) Arth.	aut-eu-form.
I, II, III on *Anemone*	
Tranzschelia tucsonensis (Arth.) Diet.	-opsis form.
I, III on *Anemone*	
Tranzschelia fusca (Pers.) Diet.	micro-form.
III on *Anemone*	

Morphological similarity among rust species does not alone necessarily indicate phylogenetic relationship. Such similarity is found, however, in so many cases among rusts occurring on closely related hosts that some significance must be attached to the phenomenon. It is now generally accepted by most students of the rusts that such correlated species are genetically related and that they have been derived one from the other. Certainly such rusts are more closely related to each other than to rusts of similar life history occurring on widely separated host families. Thus, *Puccinia abundans* (heter-eu-form with aecia on *Symphoricarpos*) is more closely related to *P. Symphoricarpi* (a micro-form occurring on the same host) than it is to any other long-cycled species of *Puccinia*. Conversely, *P. Symphoricarpi* is more closely related to the heter-eu- *P. abundans* than it is to any other micro-form.

If we accept this phenomenon of correlation as indicating immediate relationships, it is evident that in the evolutionary development of the rusts there has been a tendency to develop from one type of life cycle to another. There has, however, been very little information available to indicate the manner by which this change may have taken place. In a preceding section of this paper a number of species have been discussed which appear to be in a transitional condition as to life history. In the following pages the various types of life-cycle will be discussed and the evidence bearing on their probable inter-relationships and origin will be examined.

THE ORIGIN OF MICRO-FORMS

The micro-forms (including the lepto-forms), those which develop teliospores only, with or without accompanying pycnia, are found in all groups of the rusts and are of peculiar interest because of their evident relationship to the rusts of other life cycle. Micro-forms occur rather sparingly in the Melampsoraceae. They are common in all groups of the Aecidiaceae (Pucciniaceae), being especially abundant in the genera *Uromyces* and *Puccinia*.

The relationship of micro-forms to heteroecious eu-forms seems to the writer to furnish a clue to their method of origin, and will be discussed first.

Evidence from correlation

Some of the most important evidence bearing on the relationship of micro-forms is to be obtained from a consideration of the type of correlation which exists between species of heteroecious eu-forms and micro-forms. In such cases the correlated short-cycled form occurs on the aecial host of the long-cycled form or on related species, and the teliospores of the two forms resemble each other closely and in many cases are identical. It does not, of course, follow that all short-cycled species which occur on a host that bears aecia of a heteroecious species are correlated with the long-cycled form. Only those having similar teliospores can be so interpreted.

A list of a few such correlated species will be found in tables 3 and 7. These lists might be greatly extended, but for further specific examples the reader may be referred to the paper by Dietel (1918) dealing with this subject in which a large number of such correlations are listed. The extent to which this relationship exists in the rusts may be emphasized by pointing out the correlations which occur between genera when life histories are made the basis of generic classification. In table 4 the genera as proposed by Arthur (1906) or as used in the North American Flora (with two additions) are arranged to illustrate this sort of correlation.

TABLE 4

Generic correlations (Based on the Arthur classification)

MACROCYCLIC	MICROCYCLIC
Heteroecious	
Coleosporium	Gallowaya
Melampsoropsis	Chrysomyxa
Melampsora	Necium
Tranzschelia	Polythelis
Dicaeoma (Puccinia)	Micropuccinia
	Endophyllum
Nigredo (Uromyces)	Teleutospora
	Endophyllum
Autoecious	
Haploravenelia	Dendroecia
Uromycladium	Mcalpinia
Phragmidium	Ameris
	Teloconia
	(Micro-Phragmidium)
Dicaeoma (Puccinia)	Micropuccinia
Nigredo (Uromyces)	Teleutospora

Both heter-eu- and aut-eu-forms are included, but -opsis and brachytypes are omitted. Only genera are listed that include species which are reasonably closely correlated.

The above list, while perhaps not complete, serves to illustrate the fact that correlation between short-cycled and long-cycled forms appears in widely separated groups of the rusts.

Significance of identical hosts

It should be especially emphasized that, in the type of correlation under discussion, the host of the aecial stage of the long-cycled form and that of the correlated short-cycled form are often very closely related and in many cases identical. A considerable list of such identical hosts could be brought together. *Adoxa moschatellina* is the only known aecial host for *Puccinia Nolitangeris* as well as the only host for the short-cycled *P. Adoxae*. *Tsuga canadensis* is a common host for the aecia of *Melampsora Abietis-canadensis* and for the short-cycled *M.* (*Necium*) *Farlowii*. *Ligusticum apiifolium* is a common host for the aecia of *Puccinia Polygonivivipari* and for the correlated micro-form *P. Ligustici*. *Steironema ciliatum* is likewise a common host for the correlated *Puccinia Distichlidis* and *P. Dayi*. *Solidago serotina* and *Rudbeckia laciniata* are among the aecial hosts of *Uromyces perigynius*, and are also hosts for the correlated *U. Solidaginis* and *U. Rudbeckiae* respectively (see table 3).

This phase of the subject can, however, be best illustrated by a careful analysis of certain well-known American species. For this purpose, the correlated *Puccinia Stipae* Arth. and *Puccinia Grindeliae* Peck will first be discussed. The former species is a heter-eu-form in which the aecia occur on a long list of species of Carduaceae and Cichoriaceae and the uredinia and telia occur on a number of species of *Stipa* and related grasses. The distribution of this rust is from the Great Plains region through the Rocky Mountains and the intermountain region from Canada to Mexico. *Puccinia Grindeliae* is a micro-form which occurs likewise on a considerable number of species of Carduaceae and Cichoriaceae and has a very similar distribution. In order to bring out the host relations of this species clearly, table 5 has been prepared. In this table the hosts for *Puccinia Grindeliae* and for the aecia of *P. Stipae* are arranged in parallel columns. These hosts are taken from the material in the Arthur Herbarium and the treatment follows that given by Arthur and Fromme (1920, p. 300) and Arthur and Jackson (1922, p. 576) in the North American Flora. Species names for the hosts are listed only when they are common to the two rust species. In other cases the host genera are listed and the number

of species on which the rust has been collected is indicated. The hosts are arranged by families and tribes to bring out more clearly the host relationship.

TABLE 5

Host relationship of two correlated species

PUCCINIA STIPAE Arth. (34 aecial hosts)	PUCCINIA GRINDELIAE Peck (86 hosts)
CICHORIACEAE	CICHORIACEAE
Agoseris (2 species)	
Crepis (2 species)	
Lygodesmia juncea	Lygodesmia juncea
CARDUACEAE	CARDUACEAE
Tribe Asteraeae	*Tribe Astereae*
Aster (4 species)	
	Chrysoma (1 species)
Chrysopsis villosa	Chrysopsis villosa
	Chrysopsis (5 other species)
Chrysothamnus graveolens	Chrysothamnus graveolens
Chrysothamnus pulcherrimus	Chrysothamnus pulcherrimus
Chrysothamnus viscidiflorus (1 other species)	Chrysothamnus viscidiflorus (12 other species)
Erigeron (2 species)	Erigeron (7 species)
	Eucephalus (1 species)
Grindelia squarrosa	Grindelia squarrosa (10 other species)
Gutierrezia Sarothrae	Gutierrezia Sarothrae (7 other species)
	Gymnosperma (1 species)
	Hazardia (1 species)
	Isocoma (2 species)
	Machaeranthera (2 species)
	Petradoria (1 species)
	Prionopsis (1 species)
	Pyrrocoma (1 species)
Sideranthus grindelioides	Sideranthus grindelioides
Solidago mollis (4 other species)	Solidago mollis (7 other species)
Townsendia (1 species)	
	Xylorrhiza (2 species)
Tribe Helenieae	*Tribe Helenieae*
Hymenopappus (1 species)	Hymenopappus (1 species)
	Psilostrophe (2 species)
Tetraneuris arizonica	Tetraneuris arizonica (6 other species)
Tribe Senecioneae	*Tribe Senecioneae*
Senecio (8 species)	
	Tetradymia (4 species)

An analysis of table 5 shows that there are ten host species distributed in eight genera which are common to the two rusts, and in addition there

are two other genera which include host species for the two rusts. It will be noted that a much larger number of collections of *Puccinia Grindeliae* are available than of the aecia of *P. Stipae*. This may be accounted for by the fact that the short-cycled rust is more conspicuous over a longer period and is more commonly collected than is the aecidium. The fact that it is often difficult to obtain accurate specific identification of the host of material collected in the early part of the season may also be significant. No doubt a considerably larger list of common hosts would be found if a larger number of collections were available.

For another example, the correlated species *Puccinia monoica* (Peck) Arth. and *P. Holboellii* (Hornem.) Rostr. have been selected. The former is a heter-eu-form with aecia on Brassicaceae and the latter a micro-form occurring on the same or on related hosts. A feature especially worthy of note is that the aecial stage of *P. monoica* is systemic in the host, the aecia occurring scattered over the leaves of the somewhat more erect and slightly hypertrophied plants. The short-cycled form *P. Holboellii* has the same habit. This feature is not of uncommon occurrence and will be mentioned again. The sources of information on which the following tabulation (table 6) is based are the same as for *P. Stipae* and *P. Grindeliae* (table 5).

TABLE 6

Host relationship of two correlated species

P. MONOICA (Peck) Arth. (26 aecial hosts)	P. HOLBOELLII (Hornem.) Rostr. (23 hosts)
BRASSICACEAE	BRASSICACEAE
Arabis Crandallii	Arabis Crandallii
Arabis Drummondii	Arabis Drummondii
Arabis Lyallii	Arabis Lyallii
Arabis lyrata	Arabis lyrata occidentalis
Arabis retrofracta	Arabis retrofracta
(12 other species)	(13 other species)
	Cheiranthus (1 species)
Draba (1 species)	Draba (1 species)
Phoenocaulis (1 species)	
Schoenocrambe linifolia	Schoenocrambe linifolia
Schoenocrambe pinnata	Schoenocrambe pinnata
Smelowskia (1 species)	Smelowskia (1 species)
Sophia (3 species)	
Thelypodium (1 species)	

For these correlated rusts it will be seen that there are seven common host species distributed in two genera and two other genera which include species that are hosts for both rusts.

The close correspondence of the hosts for the aecial stage of a long-cycled heteroecious rust with those of the correlated short-cycled form emphasized in the preceding paragraphs cannot be without significance. For the present it is sufficient to point out that this phenomenon not only emphasizes the close relationship of the correlated forms, but strongly suggests that one has been derived directly from the other, and that the change has been a relatively recent one.

Occurrence of aeciospores and peridial cells in micro-forms

An interesting and important link in the evidence bearing on this subject is to be found in the occasional occurrence of aeciospores and peridial cells in the telia of short-cycled forms. The occurrence of aeciospores in such situations was apparently first pointed out by Tranzschel (1910), who recorded their presence in the following species occurring on *Euphorbia; Uromyces alpestris* Tranz., *U. scutellatus* (Schrank) Lev., *U. laevis* Koern., and *U. tinctoriicola* Magn. Dietel (1922) also notes their occurrence in *Puccinia expansa* Link, *U. excavatus* (DC.) Lev., and *Tranzschelia fusca* (Pers.) Diet. The writer has noted aeciospores and peridial cells in *P. Grindeliae* Peck and in *U. abbreviatus* Arth.

The writer first became interested in this subject in 1918 in connection with a study of *Puccinia Grindeliae*. In this species, on certain hosts and in certain collections, aeciospores and peridial cells are not at all uncommon in the telia. They are best demonstrated in collections that include a considerable number of sori that are still unruptured. The aeciospores and peridial cells are usually found in the upper part of the sorus above the teliospores. Their exact method of formation could not be traced, since only dried material has been available for examination. Their occasional presence in the young unopened sorus is, however, beyond question. The aeciospores and the peridial cells found in this species are of special interest because they resemble very closely the aeciospores and peridial cells of the correlated *P. Stipae* previously discussed. The aeciospores in the latter species are very characteristic, being large and, for aeciospores, rather thick-walled. The peridial cells are also very characteristic. The resemblance to the aeciospores and peridial cells found in the sori of *P. Grindeliae* is too remarkable to be without significance.

Kursanov (1922) also calls attention to the occurrence of peridial cells and aeciospores in the telia of *Uromyces scutellatus* and *U. laevis*. In his discussion of the former species he says:

> these cells are constructed in a typical manner not only in the structure of the cell wall, but also in that their contents includes protoplasm with two nuclei. As to the

distribution of the peridial cells, they are formed separately in indefinite parts of the fructification (more often at the periphery than near the center), so that they can not by any means play a role of protection; the aeciospores, on the contrary, are sometimes formed in short chains, but entirely normal with intercalary cells. (Translation)

It should be noted in this connection that some short-cycled forms also show urediniospores in the sori, even in species that are obviously correlated with heteroecious forms. Tranzschel (1910) has noted their occurrence in *Uromyces monspessulanus* Tranz. and *U. scutellatus* on *Euphorbia*. Urediniospores have been frequently recorded in the literature in the telia of the short-cycled *Uromyces Ficariae* on *Ficaria verna*. This species is correlated with the long-cycled *Uromyces Rumicis*, which has uredinia and telia on *Rumex* and aecia on *Ficaria*. The teliospores are essentially alike, and the urediniospores found in the telia of *U. Ficariae* show three super-equatorial germ pores as do the urediniospores of *Uromyces Rumicis*.

The occurrence of aeciospores, peridial cells, and urediniospores in the sori of short-cycled forms which are correlated with heteroecious long-cycled forms, and especially the facts brought out with reference to the close morphological resemblance of these associated inclusions to the corresponding structures in the long-cycled form, not only emphasize the close relationship of two forms so correlated but point strongly to their recent origin one from the other.

Correlation in habit between aecidial and micro-forms

Mention has previously been made, in connection with the discussion of *Puccinia monoica*, of the correlation in habit which exists between micro-forms and heteroecious eu-forms having aecia which arise from a mycelium that is systemic or perennial in the host plant. In such cases the telia of the former and the aecia of the latter appear scattered more or less evenly over the entire leaf, petiole, and stem, or in indefinite areas involving the petiole and running out along the main veins of the leaf. There is often considerable hypertrophy. For any two correlated species the habit is very much the same. Table 7 furnishes a list of a few outstanding cases of this sort among forms whose correlation is certain. The list is by no means complete and could be considerably amplified by including unconnected aecial forms which are presumably heteroecious and micro-forms of similar habit which occur on the same or related hosts.

In this connection reference may again be made also to the correlation of *Puccinia Epilobii* with the autoecious *Uromyces plumbarius* and *Puccinia Epilobii-tetragoni*, both of the latter of which have aecia that are developed from a systemic mycelium.

TABLE 7

Correlated species showing similar habit

HETER-EU-FORMS	MICRO-FORMS
Puccinia Veratri (DC.) Duby I on *Epilobium* II, III on *Veratrum*	P. Epilobii DC. III on *Epilobium*
Puccinia longissima Schroet. I on *Sedum* II, III on *Koeleria*	P. Sedi Koern. III on *Sedum*
Puccinia monoica (Peck) Arth. I on Cruciferae II, III on Poaceae	P. Holboellii (Hornem.) Rostr. III on Cruciferae
Puccinia Nolitangeris Corda I on *Adoxa* II, III on *Impatiens*	P. Adoxae Hedw. f. III on *Adoxa*
Uromyces occidentalis Diet. I on *Tithymalus* II, III on *Lupinus*	U. Tranzschelii Syd. III on *Tithymalus*
Tranzschelia punctata (Pers.) Arth. I on *Anemone* I on *Thalictrum* II, III on Amygdalaceae	Tranzschelia fusca (Pers.) Diet. III on *Anemone* Tranzschelia Thalictri (Chev.) Diet. III on *Thalictrum*

Perhaps the most outstanding example of this sort of correlation is to be found between micro-forms and the European aecial forms which occur on *Euphorbia*. These aecial forms are connected with species having uredinia and telia on the one hand on Caryophyllaceae (*Uromyces verruculosus* Schroet., *U. caryophyllinus* (Schrank.) Wint., and *U. cristatus* Schroet.), and on the other, on Fabaceae (*Uromyces Pisi* (Pers.) Wint., *U. striatus* Schroet., *U. Astragali* (Opiz.) Sacc., *U. Euphorbiae-Corniculati* Jordi). The aecial stages of all these species are systemic in the host. On the same species of *Euphorbia* there also exist several micro-forms all of which show the same habit and are correlated more or less closely with one group or the other of long-cycled forms. Those which show correlation with the series of species having the diploid generation on Caryophyllaceae include *U. scutellatus* (Schrank.) Lev., *U. cristulatus* Tranz., *U. tinctoriicola* Magn., and *U. sublevis* Tranz. Those which show correlation with the species occurring on Fabaceae include *U. alpestris* Tranz., *U. striolatus* Tranz., *U. striatellus* Tranz., *U. undulatus* Tranz., and *U. laevis* Koern. The exact specific correlations have not all been worked out (see Tranzschel, 1910).

It may be mentioned in passing that *Endophyllum Euphorbiae-sylvaticae* is undoubtedly correlated with one or the other of this group of species, and that it also is systemic in the host plant. It is worthy of mention also that there are a number of autoecious eu- and -opsis forms occurring on *Euphorbia* which are correlated with the heteroecious forms and also have aecia that develop from a systemic mycelium.

Resemblance between aecidia and micro-forms

One of the most notable features of the short-cycled forms especially in *Puccinia* and *Uromyces* is the resemblance of the telia to aecidia in their relation to the host tissue and in the grouping of the sori.

The telia in a considerable number of micro-forms are aecidium-like in their general appearance. They often arise from deep-seated primordia and resemble aecidia very closely in young stages of development. In some cases, if a collection in which the sori have not yet ruptured the host tissue is under observation, it cannot be determined without microscopic examination whether the form is an aecidium or a micro-telium. In species such as *Puccinia Podophylli* and *P. effusa* which develop two crops of telia, (see also *Uromyces Rikerianus*, *U. Suksdorfii*, and *Puccinia insperata* to be mentioned later) it is very noticeable that the early crop of teliospores and those developed in association with the aecia are of a quite different character from those of the later crop which develops from aeciospore infection. The early telia resemble aecia in their general appearance and in their relation to the host. The condensed groups of telia resulting from a single infection in many micro-forms which develop from a limited mycelium is very characteristic and resembles very closely the arrangement of the aecia in many species of *Aecidium*. In cases in which such aecia cause malformation of the host, the telia of the correlated micro-form causes a similar effect.

Fully as striking evidence on this phase of the subject has been furnished from cytological studies of the primordium of the sorus in micro-telial forms and of that of the aecia of correlated long-cycled forms. The close resemblance of the soral primordia of micro-forms in general to the primordia of aecia has been noted by a number of authors. When, however, the primordium of the telium of a particular micro-form is compared with that of the aecium of the correlated long-cycled form, the evidence of relationship is particularly striking.

Lindfors (1924) has called attention to the similarity in the early stages of the development of the primordia of the telial sori in *Tranzschelia fusca* to those of the aecia of the correlated *Tranzschelia punctata* (*Aecidium punctatum*). In speaking of the development of *T. fusca* he says:

> The development thus corresponds with that observed in aecidia, and a comparison of figure 14 with the figure given by Kursanov (1922, fig. 2, page 13) of a young stage of *Aecidium punctatum* furnishes a better illustration than any description could give of the striking similarity between the developmental stages in question.
>
> This is also the case with the aecial stage of *Ochropsora Airae*, *Aecidium leucosper mum* DC. . . . . which I have studied . . . . for the sake of making a comparison. The

agreement is actually so great that when fixing young developmental stages one must leave a part of the leaf for further development, in order that the species of the fixed material may be identified. (Translation.)

Kursanov (1922) has referred to the aecidium-like character of the telia in his report of a cytological study of *Uromyces scutellatus*, *U. laevis*, *Puccinia Asarina*, and *P. Fergussoni*. In his discussion of the last-mentioned species he says:

The process of the formation of the telium, like that which takes place in the aecidium, is typical for an entire series of forms which have been examined, among others also *Uromyces scutellatus*, and *U. laevis* already described. The resemblance is explained by the fact that the entire telium is a modified aecidium, which has been clearly demonstrated by the typical isolated cells of the peridium and by the aeciospores which are found there. (Translation.)

A brief review of the results of the cytological studies which have been made on microcyclic species has already been furnished. It is pertinent to recall at this time that in a considerable number of these the results of independent investigations have shown that, in essential features, the nuclear history is the same, up to the formation of spores, as in a typical aecidium. Both develop from basidiospore infection. The mycelium is uninucleate and the primordium of the sorus is made up of uninucleate cells. The change from the uninucleate condition to the binucleate takes place at a similar stage of development. The only difference in such cases is that, after the binucleate condition has been initiated, the microforms develop teliospores and the aecidia develop aeciospores, both diploid spore forms. Exceptions to this method of nuclear history have been noted in connection with the review of the cytological studies on microforms.

Further evidence in support of the relationship between heter-eu-forms and micro-forms might be furnished by a discussion of their geographica distribution. This phase of the subject has been adequately covered by Dietel (1918) and Orton (1927). Many supporting data are furnished by an analysis of the relative numerical occurrence and distribution of microforms as compared with long-cycled forms on the various orders and families of plants which act as their hosts. This subject has been briefly discussed by a number of authors including Kern (1915) and Orton (1927). My own contribution has been reserved for a later section of the present paper (pp. 80–90).

General discussion of micro-forms

In the foregoing account of the relationship between micro-forms and the correlated heteroecious eu-forms, as well as in the preceding sections, the discussion has been developed in considerable detail for the reason

that this relationship is considered to be the basis for a working hypothesis as to the origin of micro-forms as well as furnishing the clue to the origin or the other types of life history.

In this discussion an attempt has been made to stress the following points: (a) the existence of species at the present time which exhibit a composite or unstable life history; (b) the absence of pycinia in the majority of short-cycled forms and their erratic development in some species; (c) the presence of aeciospores and peridial cells in the sori of short-cycled forms and particularly the close resemblance of these inclusions to similar structures in the correlated eu-form; (d) the morphological resemblance between the teliospores of a micro-form and those of the correlated eu-form, and the remarkably close relationship of the hosts; (e) the gross resemblance of the telia of micro-forms to the aecia of the correlated forms, particularly in their grouping or effect on the host; (f) the close correspondence between the primordia of the sori of the two forms and the remarkable similarities in nuclear history in certain cases; and finally (g) the great variation in the details of nuclear history among the micro-forms as a whole and the evidence of extreme simplification in this regard shown in some species.

From a consideration of the significance of the facts as presented, the following deductions in the form of a series of working hypotheses are presented.

The present evolutionary tendency in the rusts appears to be toward a simplification in life history. The long-cycled forms are presumably the older, and the forms of shorter life cycle have been developed from them. This viewpoint presupposes that the group of ancestral plants from which the rusts have evolved was highly developed morphologically probably before the parasitic habit was acquired. Progressive evolution resulting in polymorphism, in a highly developed form of sexuality, and perhaps even in heterothallism, had already taken place. The more recent evolutionary tendency, perhaps strongly influenced by the simplifying effect of parasitism (Kern, 1915), has been a regressive one and has resulted in a greatly simplified sexual history and in a tendecy to the development of forms of shorter life cycle.

Much of the evidence which has been presented would seem to the writer to support the viewpoint that many microforms have been derived directly from the haploid generation of heteroecious eu-forms. The haploid mycelium developed on the aecial host may simply produce a sorus of teliospores instead of an aecium with aeciospores. These teliospores are essentially like the teliospores of the parent eu-form in morphology. The

basidiospores developed on germination, in common with those of the parent form, are capable of infecting the aecial host and give rise in the next generation to teliospores again, and thus a new micro-form is developed which continues to perpetuate itself and to bear teliospores only, and which always occurs on the aecial host of the parent macrocyclic species from which it is derived. According to this viewpoint, a micro-form of *Puccinia* or *Uromyces*, for example, is a transformed aecidium, as is indicated by the close correspondence of the developing soral primordia as well as by the nuclear history and by the occasional inclusion of vestigial aeciospores and peridial cells. Such a micro-form is in effect, then, an offshoot or life cycle mutation of the parent eu-form. In the formation of such a micro-form the parent species may not completely change to the new type of life history but may continue to exist and to carry out its orthodox life cycle as before. The two forms continue to exist as correlated 'species.'

There has been considerable diversity of opinion among previous authors with reference to the origin and relationship of the micro-forms. Two quite opposite viewpoints have been expressed. One conception is that the micro-forms represent the primitive type from which the long-cycled autoecious and later the heteroecious forms have developed, while the other opinion is that the micro-forms are reduced and derived through regression from those of longer life cycle.

The conclusion which I have reached, that the micro-forms are derived from those of longer life cycle is, in general, in line with the viewpoint of DeBary (1884, p. 308). He says, in connection with a discussion of the tremelloid Uredineae (lepto-forms):

> there remains only the assumption that they show a retrograde development by the loss of the aecidia, being descendants of aecidia-forming species and apparently homologous with certain segments of their development. (Translation.)

Dietel in his first contribution to this subject (1887) held that the primitive form was of the eu-type and that the other types of life cycle, including the micro-forms, are derived through regression. Later Dietel (1899, 1903) revised his viewpoint and for a time held that the micro-forms are primitive. More recently, however (1918), he has again returned to his earlier conclusion that the eu-forms are primitive. Blackman (1904) also reached the conclusion, based almost exclusively on cytological evidence, that the short-cycled forms are reduced and the forms possessing the aecidium are more primitive. Similar views have been held by Magnus (1898), Fischer (1904), Kern (1915), Kursanov (1922), Lindfors (1924) (in part), Orton (1927), Arthur et al., (1929), Dodge (1929), and others.

The opposite conception, that the short-cycled rusts are more primitive was perhaps first expressed by Dietel (1899) as noted above. This viewpoint has been held by Lindroth (1902), Christman (1907a), McAlpine (1906), Olive (1908, 1911b), Grove (1913b), Fromme (1914), and others. The variations in the different views held by these authors have been well reviewed by Olive (1911b), Maire (1911), and Orton (1927), and need not be repeated here.

One of the most fundamental difficulties to the acceptance of this latter point of view is evident when we consider the significance of the great variation in nuclear detail which is found among the micro-forms as a whole and the extreme simplification in this regard shown by some of them, when contrasted with the uniformity of the nuclear process as brought out by the cytological studies of the wide range of long-cycled forms. Then too, the facts presented with reference to the absence or erratic development of pycnia in so many of the micro-forms when taken into consideration with the recent remarkable discovery by Craigie (1927 a, b) of the function of pycnia in the long-cycled forms, both heteroecious and autoecious, presents a formidable obstacle to the acceptance of any theory that the short-cycled forms as they exist today are primitive.

To the writer it seems evident that two ideas have been confused. To theorize on the character of the early ancestral type of the group is one thing, but to attempt to argue that any form existing today is anything like that ancestral type is quite another matter. It is axiomatic that evolution in the rusts must at some time have progressed from the simple to the complex. The primitive ancestral type of the rusts was undoubtedly simpler in structure than the highly developed pleomorphic species with which we are now familiar. It seems most reasonable to suppose, however, that progressive evolution in the group occcurred in large part at a remote period, perhaps even before the parasitic habit was acquired. The high degree of obligate parasitism shown in the rusts today, together with the close specialization to specific host and the evidence that the rusts have evolved with their hosts, furnishes, in the aggregate, a rather convincing argument in support of the contention that the parasitic habit was acquired at a very early stage in the history of the group.

It is a commonly accepted biological principle that parasitism often has a simplifying influence (Kern, 1915). It would seem then that the parasitic mode of life in the rusts has very likely resulted not only in a profound influence upon the gross morphological features of the group but also upon the degree and type of sexuality. For these reasons it does not seem probable that any species or group of species in existence today is

likely to furnish a very adequate idea as to the character of the primitive simple ancestral type.

According to the opinion of the writer, especially in view of the evidence to be obtained from a study of correlated species, the micro-forms as they exist today merely exhibit a combination of the essential features (the change from the haploid to the diploid phase) of the aecidial stage of a long-cycled rust, with the final spore form (teliospore) and the essential features of the diploid phase (fusion of nuclei and reduction). The character of the teliospore in the micro-form is determined by the type of teliospore in the correlated parent form.

It is unfortunate that little, if any, exact knowledge is available with reference to physiologic forms in such rusts as *Puccinia Stipae* and *P. monoica* (See discussion, pp. 33–36). From the available knowledge of host specialization and physiologic forms in other species of rusts, however, it may be assumed with reasonable safety that a rust such as *P. Stipae*, which has a large number of aecial hosts, some of which are distantly related, is composed of a number of physiologic races. If this is true, it may be further suggested that the change from the long-cycled to the short-cycled form may have occurred independently in more than one race, and that correlated short-cycled forms in such cases may not have had a single time or place of origin. In support of this suggestion may be cited the microcyclic forms that are correlated with *Puccinia Andropogonis*. This species consists of a number of races having aecia on various genera of Scrophulariaceae and on the genus *Comandra* of the Santalaceae, and shows considerable variation in spore characters corresponding to the different physiologic forms. There exist on members of the Scrophulariaceae a number of micro-forms including *P. Pentstemonis* and *P. Seymeriae*, and on *Comandra*, *P. Comandrae*. All three of the species just mentioned show close correlation with races of *P. Andropogonis*, but because of slight differences in spore size and other characters it is possible to distinguish them, and they are hence treated as distinct species. They are best interpreted, however, as micro-forms derived independently from different races of the parent collective species *P. Andropogonis*. *P. Pentstemonis* occurs on *Penstemon* sp., but none of the hosts of this species are recorded as aecial hosts for *P. Andropogonis*. In the case of the other two micro-forms, however, there are three host species involved that also bear the aecia of the parent eu-form. Evidence from field observations indicates that aecia on hosts in other families are connected with uredinia and telia on *Andropogon*, indis-

tinguishable from *P. Andropogonis*. It is probable that, when more complete knowledge of the aecial hosts of this species is available, it will be possible to correlate other micro-forms with it.

The suggestion of the multiple origin of micro-forms will serve also to explain the variation in nuclear detail which occurs in certain species and which has been noted previously in connection with the review of the cytological studies of microcyclic forms. It has been shown that much variation in nuclear detail is found among the short-cycled forms as a whole, and that there is evidence that considerable variation of this sort may occur as between different strains or races of the same species. When the evidence that the rusts have developed with their hosts is taken into consideration, together with the known facts with reference to specialization and the existence of physiologic races and forms, it is rather to be expected that microcyclic forms might develop from different races of the parent form, or in different regions, in the same race. For these reasons it is not surprising that micro-forms show great variation as a whole and that decided differences may occur in the nuclear history even in the same species.

While a large number of the short-cycled forms may have arisen from heteroecious eu-forms in the manner suggested, some may have been derived in an entirely similar manner from autoecious species, as, for example, the microcyclic rusts on *Rosa* to be discussed later. It seems probable, however, that the origin of micro-forms from autoecious rusts has commonly followed a somewhat different course of development through -opsis and brachy-forms. This phase of the subject will be given more attention in connection with the discussion of the origin of the -opsis and brachy-forms. In deriving micro-forms from the haploid generation of heteroecious species, I have perhaps fallen into the error of assuming that the change was an immediate one. As will be shown in connection with the discussion of -opsis forms, there is considerable evidence to indicate that the change has been a gradual one in many cases.

Most of the examples which have been cited in the preceding discussion have been taken from the Aecidiaceae (Pucciniaceae). There would appear to be no reason, however, why the same argument may not apply in deriving short-cycled forms in other groups of rusts. Accordingly, *Gallowaya pinicola* may be interpreted as a micro-*Coleosporium* derived from the haploid phase of some species of heter-eu-*Coleosporium* having aecia on *Pinus*. Similarly, *Necium Farlowii* may be interpreted as a short-cycled *Melampsora*. It occurs on *Tsuga*, a known aecial host for the heteroecious *Melampsora Abietis-candensis*. *Chrysomyxa Abietis* and other similar species may have been derived from the haploid generation of

heter-eu- species of *Chrysomyxa*. These species occur on *Picea*, the aecial host for the heter-eu-forms. Lindfors (1924), while accepting in general the origin of microcyclic forms as derived through reduction, singles out *Chrysomyxa Abietis* as an exception and attempts to show that it may be regarded as a primitive type. It is not clear to the writer why this form does not bear the same relation to the long-cycled forms of *Chrysomyxa* (*Melampsoropsis*) as do the microcyclic forms of *Uromyces* and *Puccinia* to the correlated eu-forms.

It is noticeable that no short-cycled forms are known which are correlated with the heteroecious genera *Pucciniastrum*, *Hyalopsora*, *Uredinopsis*, *Milesia*, *Melampsorella*, and *Calyptospora*, all of which develop their aecia on *Abies* or *Tsuga* and their teliospores internally in the host tissues, either in the mesophyll, just beneath the epidermis, or in the epidermal cells, often not forming a sorus in the usual sense of the term.

Should a micro-form develop from any of these genera on the aecial host, it would presumably be very inconspicuous and not easily identified as a rust unless it were in a germinating condition. If such a form were collected it might very easily be discarded as a sterile leaf spot by the general mycologist and even by the rust specialist unless he had this sort of thing in mind. Such micro-telial forms might merely show as yellowish or brownish spots on the *Abies* leaves with no external evidence of a fruiting structure. Their true nature could be determined only by careful sectioning and germination studies. It seems quite reasonable to expect that some short-cycled forms have been developed from one or more of the long-cycled genera mentioned above, and that such species may exist not uncommonly on *Abies* but that they have been overlooked or their true nature has not been determined.

In this connection attention may be directed to the very interesting fungus *Meria Laricis* Vuill. (*Hartigiella Laricis* (Hartig) Sydow) which occurs on the leaves of *Larix europea* in Europe. This species has been assigned a doubtful position in the Ustiliganales, or is included in the Hyphomycetes. The fact that this fungus occurs on the leaves of *Larix*, together with its structure and the method of development of the spores, as brought out in the figures of Vuillemin (1905), is strongly suggestive that a reinvestigation of its morphology and a study of its nuclear history may show that its real relationship is with the rust genus *Melampsoridium*, which is known to have aecia on *Larix*.

The Raveneliatae and Phragmidiatae are all autoecious with the exception of the primitive genus *Tranzschelia*. In this group short-cycled forms exist which are presumably in large part developed through the

brachy-forms, as, for example, *Calliospora* from *Uropyxis*, *Tricella* from *Phragmapyxis*, *Mcalpinia* from *Uromycladium*, *Nephlyctis* from *Prospodium*, and *Dendroecia* from *Ravenelia*.

In the Phragmidiatae there is a very interesting series of rust species occurring on the genus *Rosa*. The larger number of species on this host are aut-eu-forms with caeomoid aecia assigned to *Phragmidium*. It is a characteristic feature of the aecia of some species to become more or less locally systemic in the leaves, petioles, and stems, and even in some cases to appear to be perennial.[7] Three very interesting microcyclic rusts occur on *Rosa* in various parts of the northern hemisphere. All are systemic in the host, causing witches' brooms, possibly even perennial. All have the same general habit and manner of development as the aecia of some of the eu-forms. One of these develops one-celled teliospores. This form was first named *Uromyces rosicola* E. & E., and later was made the basis of the monotypic genus *Ameris* by Arthur. It is a rare species, known only from a few collections from the plains and Rocky Mountain regions of North America. The second form develops two-celled teliospores and was originally described as *Puccinia Rosae* Barcl. It was transferred to *Gymnoconia* by Liro and more recently made the basis of the genus *Teloconia* by Sydow. It occurs throughout eastern Europe and Asia on various species of *Rosa*. The third form develops *Phragmidium*-like teliospores. It was named *Phragmidium devastatrix* Sorok. It is apparently rare and known only on *Rosa lutea* in central Asia.

According to the interpretation of the writer it seems probable that from the haploid generation of long-cycled *Phragmidium* species on *Rosa* there have developed three distinct types of micro-forms, differing primarily in the number of cells in the teliospore, which are now classified in three different genera. All have the same systemic habit. Pycnia are unknown in *Ameris* but are present in the other two species. These are subcuticular as in *Phragmidium*. Multiple germ pores are present in *Ameris* and in *P. devastatrix*, though the pores are obscure in *Teloconia*. All three forms would appear to have originated in the same manner as the micro-forms of *Puccinia* and *Uromyces*, i.e., from the haploid generation of the eu-forms. The variable number of cells in the teliospore may be interpreted as variations from the many celled *Phragmidium* type which have developed in the process of simplification to a micro-form, and very probably indicates that *Phragmidium* originated from an ancestral type which possessed two-celled teliospores.

[7] *Gymnoconia Rosae-gymnocarpae* (Diet.) Arth., based in error on the aecial stage of *Phragmidium Rosae-californicae* Diet., is a case in point.

It should be recognized that many microcyclic species are known which cannot be correlated with any macrocylic form. Any attempt to work out correlations is limited by the incomplete state of existing knowledge with reference to the full life cycle of many heteroecious rusts. In many cases, also, the parent eu-form has probably disappeared and the microcyclic form derived from it now stands alone. In other cases, it is conceivable that there may have been a gradual change in the structural characters of the teliospores since their origin, and that because of this their relationship can no longer be traced.

THE ORIGIN OF ENDOPHYLLUM AND RELATED FORMS

The essential features of the morphology of the sorus in *Endophyllum* are the same as in *Aecidium* except that the spores have taken on the function of teliospores and germinate by the development of basidia and basidiospores. In the typical *Endophyllum* the nuclear phenomena are the same as for aecidia to the time of germination of the spores, and the nuclear history is comparable to that of many micro-forms of *Puccinia* and *Uromyces*.

The species of *Endophyllum* and other endo-forms show remarkable correlation with heter-eu-forms as well as with -opsis and micro-forms in some cases. Table 8 has been prepared to illustrate these relationships and to serve as a basis for the detailed discussion which follows.

It will be noted that the list includes as correlated forms, not only the related eu- or -opsis forms but also micro-forms where they exist. In discussing the significance of these correlations, the different species of *Endophyllum* will be taken up separately and their relationship will be reviewed in some detail.

Endophyllum tuberculatum (Ell. & Kell.) Arth. & Fromme occurs on species of Malvaceae (*Althaea*, *Callirhoë*, *Sidalcea*) in the plains region of North America from Wyoming to Oklahoma. The aecia are developed on a perennial mycelium which becomes systemic in the stems and leaves of the host, commonly occurring along the veins. Pycnia are unknown in this species. The shape and method of dehiscence of the aecia of the *Endophyllum*, and the shape and markings of the peridial cells as well as of the spores are remarkably like the corresponding structures in the aecia of *Puccinia interveniens* (Peck) Bethel, a heter-opsis form occurring in western North America and in South America, having aecia on Malvaceae and telia on *Stipa* and related grasses. In *P. interveniens* the aecia develop from a limited mycelium, a condition which does not hold for the aecia of other forms correlated with *Endophyllum* species. There

is no known heter-eu-form in this series. There are, however, three autoecious rusts on *Stipa*, namely: *Puccinia graminella* (Speg.) Diet. & Holw., an aut-opsis form occurring in both North and South America; *P. digna* Arth., and *Uromyces pencanus* Arth., both the latter aut-eu-forms recently described from South America (Arthur, 1925). The aecia and aeciospores of all three of these species are very much alike, as well as the urediniospores, where present, and the teliospores are of similar character. They obviously represent a series of closely correlated species. Furthermore, the aecia of these autoecious *Stipa* rusts correspond very closely to the aecia of the heter-opsis *Puccinia interveniens* on Malvaceae and to the aecia of *Endopyllum tuberculatum*. In *Puccinia Sherardiana* Koern., a micro-form occurring on Malvaceae, the teliospores correspond in morphology to the teliospores of *P. interveniens* as well as to those of the autocious *Stipa* rusts. There is some variation in spore size and wall thickness, but the general characters and the markings of spores and peridial cells are so close as to leave no doubt that the several species in the series are all genetically related.

It may be mentioned in passing that these species are the only autoecious or heter-opsis rusts known on Poaceae. The facts that they all occur on *Stipa* or related hosts and that they are closely correlated among themselves and with *Endophyllum tuberculatum* and the micro-form *Puccinia Sherardiana*, make them a very interesting and important group and there will be occasion to mention them again in other connections.

Endophyllum Euphorbiae-silvaticae, which occurs on *Euphorbia amygdaloides* (*E. silvaticae*) throughout central Europe, develops from a perennial mycelium which becomes systemic in the host and agrees closely in all its characters with *Aecidium Euphorbiae* Pers. (collective) which is now known to consist of a number of distinct forms which, while essentially identical in morphology, are connected with a number of distinct species of heter-eu-*Uromyces* occurring on Fabaceae, including *U. striatus*, *U. Pisi*, *U. Astragali*, *U. Genistae-tinctoriae* and others. The aecia of these species are all systemic in the host and, as previously noted, a series of micro-*Uromyces* is known on *Euphorbia*, the teliospores of which correspond in morphology to those of the heter-eu-forms on Fabaceae. All these species develop from systemic infections.

Endophyllum Sempervivi occurs throughout central Europe on various species of *Sempervivum*. It also is perennial in the host and has been introduced on plants imported from Europe into the eastern United States. No heter-eu-form is known having aecia on *Sempervivum*, but there exists an unconnected aecidium in southern France on *S. tectorum* which

TABLE 8

Correlation of endo- forms

EU-FORMS	-OPSIS FORMS	MICRO-FORMS	ENDO-FORMS
	P. interveniens I on Malvaceae III on *Stipa* (heteroecious)	P. Sherardiana III on Malvaceae	Endophyllum tuberculatum on Malvaceae
Uromyces pencanus Puccinia digna I, II, III on *Stipa* (autoecious)	P. graminella I, III on *Stipa* (autoecious)		
Uromyces striatus U. Pisi U. Astragali U. Genistae-tinctoriae I on *Euphorbia* II, III on Leguminosae	U. excavatus I, III on *Euphorbia*	U. striolatus U. striatellus U. alpestris U. undulatus III on *Euphorbia*	E. Euphorbiae-sylvaticae and the var. uninucleatum on *Euphorbia*
Endophyllum Sempervivi var. aecidioides I on *Sempervivum* (an unconnected Aecidium)			E. Sempervivi on *Sempervivum*
P. longissima I on *Sedum* II, III on *Koeleria*		P. Sedi III on *Sedum*	
Aecidium Valerianellae I on *Valerianella* (an unconnected Aecidium) II, III on ?	P. commutata I, III on *Valeriana*	P. Valerianae III on *Valeriana*	E. Valerianae-tuberosae on *Valeriana* E. Centranthi-rubri on *Centranthus*
	Gymnoconia interstitialis I, III on *Rubus*		Kunkelia nitens on *Rubus* several forms (Dodge, 1923a, 1924; Dodge and Gaiser, 1926)

TABLE 8 (continued)

EU-FORMS	-OPSIS FORMS	MICRO-FORMS	ENDO-FORMS
Trazschelia punctata I on *Anemone*, *Thalictrum* II, III on *Prunus* etc.	T. tucsonensis I, III on *Anemone*	T. fusca III on *Anemone* T. Thalictri III on *Thalictrum*	Aecidium punctatum on *Anemone* Uninucleate form (Kursanov, 1922)
Ochropsora Sorbi I on *Anemone* II, III on *Sorbus*			Aecidium leucospermum on *Anemone* Uninucleate form (Kursanov, 1922)
Cronartium flaccidum I on *Pinus sylvestris* II, III on various hosts			Peridermium Pini on *Pinus sylvestris* Repeating form (Haack, 1914; Klebahn, 1918)
Cronartium Harknessii I on *Pinus contorta* etc. II, III on Scrophulariaceae			Peridermium on *Pinus contorta* etc. Repeating form (Meinecke, 1920)
Cronartium Quercus I on *Pinus* spp. II, III on *Quercus* spp.			Peridermium on *Pinus radiata* etc. Pacific Coast form (Meinecke, 1916, 1920)
Cronartium sp. I on *Pinus* II, III on (?)			Peridermium on *Pinus sylvestris* The 'Woodgate rust' (York, 1926)

Maire (1900, 1902) has described as *Endophyllum Sempervivi* var. *aecidioides*. He showed that the spores germinate like aeciospores and that, while he could infect the host with the typical form, he could not do so with the variety. This variety has all the characters of the typical form except that the method of germination of the spores is like that of an aecidium. Just why Maire described this as a variety of the *Endophyllum* when he had such convincing evidence that this was an aecidium of a heteroecious species is difficult to explain. The form has largely been overlooked on this account and has apparently never been transferred to the form genus *Aecidium*. While the full life history of this aecidium is unknown, it serves the purpose of this discussion just as well as though its life history had been determined. The fact that it was described as a variety of *E. Sempervivi* serves to emphasize the very close correspondence in morphology between *Endophyllum* species and the aecia of correlated heter-eu-forms. Of interest in this connection is an aecidium which occurs on the closely related host *Sedum*. Because of its resemblance in general characters to *Endophyllum Sempervivi*, it was at one time named *E. Sedi* (DC.) Lév. This species is also systemic in the host plant. It is now known to be the aecial stage of *Puccinia longissima* Schroet., which has uredinia and telia on the grass, *Koeleria*. On *Sedum* there also exists a rare micro-form *Puccinia Sedi* Koern., having the habit of the *Aecidium* and the *Endophyllum*, whose teliospores resemble closely those of the heter-eu-form.

Endophyllum Valerianae-tuberosae occurs in France on *Valeriana tuberosa*. It also is systemic in the host plant. There exists also an unconnected aecial form, *Aecidium Valerianellae* Biv. on various species of *Valerianella*, which corresponds closely in habit and in essential morphological characters with the *Endophyllum*. This *Aecidium* is obviously heteroecious, though the connection has not been established. There exists on *Valeriana* also in both Europe and America an -opsis form with repeating aecia, *Puccinia commutata* Syd., which is correlated. *Puccinia Valerianae* Carest., a micro-form, may also be correlated. Its teliospores are presumably like the teliospores of the unknown eu-form to which *Aecidium Valerianellae* belongs.

The only other known species of *Endophyllum* which occurs in temperate regions is *E. Centranthi-rubri* Poir. It also develops from a systemic mycelium. This species is found in southern Europe on *Centranthus Calcitrapa* and *C. rubrum*. The host genus bears no other rusts. It is, however, very closely related to *Valeriana* and *Valerianella*. The *Endophyllum* is also very similar in its gross morphological characters to *E. Valerianae-*

tuberosae. It is quite probable that in origin and relationship it is similar to the latter species.

The above-listed forms include all the known *Endophyllum* species occurring in temperate regions. It will be noted that each of them develops from a systemic, presumably perennial mycelium, and that all show close correlation with aecial forms of heteroecious species as to host, habit, and morphology.

From a consideration of the evidence given above together with some to be furnished later I would venture the hypothesis that the species of *Endophyllum* and other *Endophyllum*-like forms are to be derived directly from the haploid generation of long-cycled forms. In the case of the *Endophyllum* species which have been discussed, they are all to be derived from the haploid generation of heteroecious species of *Puccinia* or *Uromyces*. There would appear to be no reason, however, why they could not be so derived from autoecious species. It would appear also that *Endophyllum*-like forms may occur in other groups of rusts.

In the typical *Endophyllum* the shortening of the life cycle has taken place by the fusion of the two nuclei in the aeciospore, which necessitates the immediate development of a basidium in order that reduction may take place. As has been shown in the cytological review of the species of *Endophyllum*, however, this typical condition is rarely realized, and much variation in nuclear history is found in this group.

According to this explanation of their origin, the species of *Endophyllum* are related genetically to *Puccinia* or *Uromyces* and represent a special life-history type comparable to the -opsis, brachy-, and micro-forms. This explanation is essentially the view held by Tranzschel (1904). Fromme (1914) also held the view that *Endophyllum* represents a reduced form, derived from the haploid generation of heter- or aut-eu-species, without, apparently, recognizing the close correlation with existing long-cycled forms.

Barclay (1891) is usually credited as being the first to suggest that *Endophyllum* might be a primitive type from which the other rusts are derived. A careful reading of his excellent paper, however, shows that, while he analyzed such a possibility in considerable detail, he finally rejected the hypothesis as improbable. Grove (1913b), however, has more recently revived this hypothesis. The analysis of the endo-forms as given in the preceding pages would seem to offer no support for this contention.

In addition to those already discussed, a number of species of *Endophyllum* are reported from tropical or subtropical regions. These include *E. Griffithiae* (P. Henn.) Racib., *E. Dichroae* Racib., and *E. Ixorae* Gäum.

reported from Java, *E. MacOwani* Pole-Evans from southern and central Africa, and the species described by Olive and Whetzel (1917) from Porto Rico—*E. circumscriptum* (Schw.) Wh. & O., *E. Wedeliae* (Earl) Wh. & O., *E. decoloratum* (Schw.) Wh. & O., and *E. Stachytarphetae* (P. Henn.) Wh. & O. None of these species has yet been correlated with other forms, presumably because of our limited knowledge of tropical rusts and of the lack of any amount of cultural work with the rusts of tropical regions. It is worthy of note that these names, with two exceptions, are based on rusts previously described as species of *Aecidium*. It should be noted, also, that each species listed above develops from a limited mycelium. None of them, so far as I have been able to determine, shows any evidence of being systemic in the host. It is probable that many more species of *Endophyllum* exist in the tropics. Those who have the opportunity would do a great service to uredinology by studying the germination of the spores of tropical aecidial forms.

One of the most interesting points with reference to the *Endophyllum* species which occur in temperate regions is that they are all systemic and perennial in the host plant, as has been emphasized above. No proven species of *Endophyllum* exists in temperate regions which is not perennial. The only species of *Endophyllum* known which develop from a limited infection are tropical or subtropical. The question arises as to whether any significance should be attached to this circumstance. On account of the character of the spores of all species—relatively thin-walled, germinating as soon as mature, and not adapted to a resting period—it seems reasonable to assume that no species of *Endophyllum* could maintain itself in temperate regions unless it were derived from a perennial aecidium or had acquired the perennial habit as soon as it was derived. In the tropics, however, a species derived from an aecidium with limited mycelium would be able to survive, and the perennial habit would not be essential to its continued existence. The writer would venture to suggest that it is not unreasonable to assume that an endo-condition may not uncommonly develop in temperate-region species of *Aecidium* having a limited mycelium. Such a form, because of the absence of the perennial habit, would be unable to survive and hence would remain unobserved.

It would be interesting to test this hypothesis by an extended experimental study of the forms which show evidence of mutability, especially certain -opsis forms such as *Puccinia effusa* and others to be discussed later. A fruitful field might also be found in the study of the aecia of such species as *P. Stipae*, *P. monoica*, and of other eu-forms which show abundant correspondence in hosts with correlated micro-forms. Since all tem-

perate-region species of *Endophyllum* develop from a perennial mycelium, it would seem probable that many more endo-forms exist among aecidial forms of similar habit than have been recognized. Reference has already been made to the uninucleate forms of *Aecidium punctatum* and *A. leucospermum*. A search for such endo-forms among species of heter-eu-forms having perennial aecia would, in all probability, be fruitful of results.

It is the common practice, particularly with reference to the tropical species of *Endophyllum*, once the germination has been tested, to refer to the *Endophyllum* all the collections and records of the species. In view of the present study and of the correlations pointed out, this procedure seems quite illogical. Without exception, the studies which have resulted in assigning a tropical aecidium to *Endophyllum* have been limited in scope and relatively few collections have been germinated, often from a single locality. Is it not more reasonable to admit the probability that both forms may still exist—the aecidium of a heteroecious rust and the derived *Endophyllum*? Of course it is possible that some forms of *Endophyllum* exist as isolated forms, the parent forms from which they were derived having disappeared.

Perhaps the clearest case of the relationship of endo-forms is to be found in *Kunkelia nitens* and its relation to *Gymnoconia interstialis*. The latter is an aut-opsis form occurring on *Rubus* which has a systemic and perennial caeomoid aecium. Its relationship is with the Phragmidiatae. Kunkel (1913, 1914) was the first to show that a short-cycled form exists which has all the characters of the aecium of the typical form except that the spores germinate with a four-celled promycelium. Dodge (1923, 1924) and Dodge and Gaiser (1926) have studied these species in considerable detail both culturally and cytologically, and have shown that not one but several short-cycled forms exist, all having the gross morphological characters of the aecia of the parent species but differing in minor details of spore size, color, or relative abundance or absence of pycnia or in fundamental cytological details (see review, p. 25). Dodge clearly recognized that these forms are derived from the haploid generation of the *Gymnoconia*. *Kunkelia* is properly interpreted as an endo-form with the gross morphology of a caeoma.

The endo-Peridermiums

This review of endo-forms would not be complete without mention of the repeating forms of *Peridermium* which have been described. Haack (1914) was the first to present evidence that a form of *Peridermium* on

Pinus sylvestris occurs in central Europe which is capable of passing from pine to pine. Klebahn (1918) amply confirmed Haack's results. This species is known as *Peridermium Pini* (Willd.) Kleb. In the meantime Meinecke (1916) presented evidence indicating that a similar situation exists in the Pacific Coast form of the *Peridermium* on *Pinus radiata* which has been referred to *Cronartium Quercus* (Brond.) Schroet. In a later publication Meinecke (1920) amply confirms his previous results and shows that a similar situation exists in the gall form of *Peridermium* occurring on *Pinus contorta*, *P. ponderosa*, *P. Jeffreyi*, etc., which has been referred to the *Cronartium* now known as *C. Harknessii* (Moore) Meinecke, having uredinia and telia on *Castilleja* and other members of the Scrophulariaceae. The evidence that repeating forms of these species of *Peridermium* exist is conclusive (see also Dodge, 1929). There can be little doubt that the *Periderium* recently reported by York (1926) on *Pinus sylvestris* from near Woodgate, New York, is also such a repeating form. It is apparently not the same as the form studied by Klebahn, though occurring on the same host.

It is of special interest to note that Klebahn found that pycnia are not always produced in the form which he studied and Meinecke reports that pycnia are unknown in the Pacific Coast form of *C. Quercus* and that he has found rarely only abortive pycnia in the repeating form of *C. Harknessii*. Both authors have described the germination of the spores as typically aecioid with no evidence of a promycelium.

Unfortunately none of these forms has been studied cytologically, and the nuclear phenomena are unknown. In spite of this fact and of the reported aecioid germination of the spores, I should interpret these forms as exhibiting an endo-condition and as being derived in the same way as the typical Endophyllums; on this account I have included them in the table of correlations.

In the early part of this paper the cytological work on micro- and endoforms has been reviewed. It is evident from this review that in the development of these reduced forms from the eu-forms a number of variations in the nuclear phenomena have arisen. Uninucleate forms occur in a number of cases. Even though fusion cells occur, resulting in conjugate nuclei in the spores, these nuclei may fail to fuse, as in the typical form of *Endophyllum Euphorbiae-sylvaticae* and in one form of *Kunkelia nitens*. Where the forms are uninucleate (with the exception of *E. Euphorbiae-sylvaticae var. uninucleatum*), the basidium is reduced to two cells. Where no fusion of the nuclei occurs there is no possibility of a reduction division. As Dodge (1924) has pointed out, the development of a four-celled

basidium is definitely associated with the necessity for chromosome reduction. Where reduction no longer occurs, as in uninucleate forms, a two-celled basidium is commonly developed. Is it not entirely logical, then, to expect that a further step in simplification may take place in forms in which the reduction division has been lost? It is quite conceivable that in some endo-forms the development of the basidium is dispensed with entirely and that there occurs, to all outward appearances, an aecial form repeating itself on the aecial host.

The hypothesis may be advanced, then, that these repeating Peridermiums are endo-forms, derived from the haploid generation of species of *Cronartium*, in which the reduction division no longer occurs, and which because of this fact have been further simplified by the loss of the basidium.

It seems probable that this explanation will also apply to the uninucleate races of *Aecidium punctatum* and *A. leucospermum* studied by Kursanov (1922), which have been previously mentioned. On this account these forms are, also, included in the table of correlations. Kursanov reported the latter as germinating in a manner typical for aeciospores, while Soppitt (1893) has shown that it is capable of repeating itself on *Anemone*. Both these aecidia are the aecial stages of known heteroecious rusts and both are systemic and presumably perennial. The last observation applies to the uninucleate forms as well.[8]

In deriving the micro- and endo-types from the eu-forms in the manner described, it should be emphasized that these microcyclic forms have had their origin in a change which occurred in the sorus that developed on the haploid thallus. In the micro-forms teliospores develop in the place of aeciospores. In the endo-forms the function of teliospores is assumed by the aeciospores. In both cases we have a similar result. A microcyclic form has developed from an eu-form. In the typical forms, such as *Puccinia Malvacearum*, *Endophyllum Sempervivi*, and *Tranzschelia fusca* the essential points in the life cycle of the parent eu-form—the initiation of the diploid phase, fusion of the nuclei in the teliospore, and the reduction divisions which follow in the formation of the basidium—are brought as close together as may be on the same thallus. The entire diploid thallus is eliminated, together with the repeating conidial stage. Pycnia may or may not be retained. The uninucleate forms, those which are binucleate

[8] In this connection the case of *Uromyces Cunninghamianus* as described by Barclay is of peculiar interest. If the repeating forms of *Peridermium* and of the species of *Aecidium* mentioned above are to be interpreted as endo-forms, what of the -opsis forms of *Uromyces* and *Puccinia* which have been determined to have so-called repeating aecidia? (See discussion pp. 67–72.)

throughout, and those in which the fusion nucleus and reduction division are lost, may be interpreted as variations that have developed in the further process of reduction.

THE ORIGIN OF -OPSIS FORMS

The explanation of the origin and relationship of the -opsis forms is somewhat more difficult and involved than is that of the micro- and endoforms which have already been discussed. In general, however, the evidence that will be presented would indicate that the -opsis forms have not, as has been commonly assumed, arisen from the eu-forms by the simple process of dropping the uredinial stage.

Transitional -opsis forms

It would seem reasonable to expect that some of the -opsis forms might be derived by direct origin from the haploid phase of heteroecious euforms as outlined above for the microcyclic ones. In such cases both the aecia and the telia might be retained in the resulting form. The evidence to be gained from a study of -opsis forms occurring on the aecial hosts of correlated heter-eu-forms, or of those occurring on the same hosts as micro-forms clearly derived from heteroecious forms, will first be presented.

As the first example of such a form may be cited the peculiar relation existing between *Puccinia Cryptotaeniae* Peck and *P. microica* Ellis, both of which occur on *Deringa* (*Cryptotaenia*) *canadensis*. The former, common in the north eastern United States, is one of the micro-forms which may or may not develop pycnia in association with the telia. The latter species is very rare, being known only from two collections, one from Maryland in the vicinity of Washington, D. C., and the other from Decorah, Iowa. In these collections aecia occur in association with the telia, and the species has been considered an -opsis form. The telia and teliospores are alike in the two species. In *P. microica* it is noteworthy that the aecia occur only at the margin of many of the groups, and obviously mature later than some of the associated telia. They are, however, evidently borne on the same mycelium. In some of the groups no aecia are developed. In some others, aecia predominate over the telia, though this is apparently exceptional.

Unfortunately, these two rusts on *Cryptotaenia* are the only ones known on this host and the species cannot be correlated. The character of the teliospores, however, strongly suggests that the relationship is with the rusts on *Polygonum* which have aecia on umbelliferous hosts. *Puccinia*

Cryptotaeniae is apparently a micro-form related to a heter-eu-form having its diploid generation on Polygonaceae, the haploid generation of which at one time occurred on *Cryptotaenia* or one of its immediate ancestors.

The occasional occurrence of aeciospores and peridial cells in the sori of micro-forms has already been discussed. *Puccinia Cryptotaeniae* is apparently a form which occasionally develops fully formed aecia, thus furnishing a clue to the possible origin of some -opsis forms from heter-eu-forms in the same manner that has been described for the micro-forms except that both aecia and telia have continued to develop. In the case of the two forms under discussion it would seem to be very questionable whether *P. microica* should be interpreted as a 'species' distinct from *P. Cryptotaeniae*. It would seem rather to represent a case in which aecia are occasionally developed in an otherwise typical micro-form.

Puccinia consimilis Ell. & Ev. has been considered to be an -opsis form. This rare species occurs on *Schoenocrambe linifolia*, and the only collections of which I have any knowledge were made in 1887, 1889, and 1891 in the vicinity of Helena, Montana. This rust occurs as a systemic infection in the host, pycnia, aecia, and telia being intermingled and breaking out over the entire surfaces of the leaves of infected plants. The aecia and aeciospores are like those of the heteroecious eu-form *P. monoica*. The telia are like those of the micro-form *P. Holboellii*, while the teliospores are like those of both the micro- and the eu-form. The aecia of the eu-form and the telia of the microform also both develop from a systemic infection, as previously noted, and both are known on the same host species as the –opsis form. These three species then represent a series of correlated forms. The micro-form has presumably been derived from the aecia of the heter-eu-form, and the -opsis form perhaps represents a transitional condition in the development of the micro- from the eu-form in which the aecidial structure is retained. It is of interest to note that in this form teliospores occur abundantly in the aecial cups, which fact would seem to dispose of any argument that *P. consimilis* represents merely a simultaneous and independent infection by the micro- and the eu-form in the same host plant.

If the interpretation above suggested is the correct one, then it is questionable whether a form which shows such a transitional condition should be treated as an independent species.[9]

[9] It would be illuminating to have a careful cultural and cytological study of this 'species.' How do the aeciospores function? There is no evidence that they give rise to a scattered, limited infection of telia on the same host as would be the case in a typical -opsis form. Is it possible that they still retain the ability to reinfect the alternate hosts of the parent eu-form and continue the normal cycle? In view of the method of origin of endo-forms discussed previously, is it pos-

Some of the rusts occurring on Ranunculaceae are of interest in this connection. Among the rusts having their diploid thalli on Poaceae are a number with aecia on ranunculaceous hosts. Chief among these are *Uromyces Dactylidis* Otth., *U. Poae* Rabh., *Puccinia Clematidis* (DC.) Lag., *P. borealis* Juel, and *P. Magnusiana* Koern. Of the species named, one of the most common and widespread is *P. Clematidis*. As interpreted by Arthur and Fromme (1920), this species is a collective one made up of a considerable number of physiologic races, many of which have been described as separate species and are still so treated by some modern authors. *P. Clematidis* is characterized by having telia long covered by the epidermis, which in general does not become ruptured. Accompanying the telia of some strains there is more or less development of stroma or of paraphyses, which may be entirely absent in other forms. The spores also vary to a considerable extent, especially in size and in thickness of wall.

The variable nature of this collective species makes it difficult to work out exact correlations. There exist on Ranunculaceae, however, a number of micro-forms which because of the character of their telia and shapes of their spores suggest a relationship with *Puccinia Clematidis*. Among these are *Puccinia Pulsatillae* Kalchbr. (*P. DeBaryana* Thüm.), *P. Anemones-virginianae* Schw., and *P. rhytismoides* Johans.

Of special interest for the present purpose, however, is an -opsis form, *Puccinia gigantispora* Bubák, which occurs in the western United States on *Anemone globosa*, the morphology of which suggests a relation to *P. Pulsatillae* and to *P. Clematidis*. This -opsis form possesses pycnia in association with the aecia, though it is noticeable that the pycnia are frequently lacking. A feature of this species is that telia are frequently associated with the aecia from the same infection. Pycnia have been assumed to be lacking in such conditions, and the species is one that has been considered to possess repeating or diploid aecia, telia developing only with aecia of this type. A careful examination of all the material available in the Arthur Herbarium has convinced the writer that this explanation is not the correct one. Pycnia have been observed in a number of

sible that in such a transitional form the influence which has resulted in a partial change to a micro- type of life history has also affected the aecia so that the aeciospores function also as teliospores and we have the initiation of an *Endophyllum*? The aecial stage in the form under discussion develops from a systemic and presumably perennial infection, and it is entirely possible that an endo-form derived from it would be able to perpetuate itself through infection of seedlings or of dormant buds. While admittedly purely speculative, the suggestions implied in the above questions are inserted here to emphasize the wealth of problems awaiting solution in this field, and the promise of important and fundamental results to be derived from a thorough study of such transitional forms.

cases in association with the groups composed of both aecia and telia. Such an infection is certainly primary. One collection was preserved, consisting of an entire plant, heavily infected. In this collection, where the infection occurred on the younger leaves, aecia predominated and were usually accompanied by pycnia, rarely by telia. On older leaves few of the spots showed pycnia, but aecia were accompanied quite regularly by telia. On still older leaves the spots were composed largely of telia with a few aecia, or of telia only. Where infection occurred on the petioles, especially of older leaves, the spots developed telia only or telia with a very few aecia, often only one or two. A comparison of the condition of the aecia on the youngest tissues with those on the older showed that they were of the same stage of development and strongly indicates that the infection on this plant occurred all at one time and was all primary (i.e., from basidiospore infection). An examination of all the other collections of this species leads to the conclusion that all the infection is primary and none from aeciospores. This species then is not a true -opsis form but is comparable to *Puccinia consimilis*. While its exact correlation cannot be traced, it is a form probably derived from the haploid generation of some heteroecious grass rust having aecia on Ranunculaceae, possibly one of the races of *P. Clematidis*, and represents a transitional condition in the development of a micro-form in which the aecia are still retained.

Puccinia (*Allodus*) *opposita* Orton is a similar species also found on *Anemone globosa*, and its origin may be explained in the same way.

Among the rusts on Onagraceae the -opsis form *Puccinia Jussiaeae* Speg. is similar to those previously mentioned. In this species, as treated in the North American Flora, a number of species of *Ludwigia* are recorded as hosts. Telia, however, are present in the specimens available only on *Ludwigia polycarpa* and on the South American *Jussiaea longifolia*. All of the fifteen collections in the Arthur Herbarium on seven other host species show aecia only. All three collections on *Ludwigia polycarpa* show telia, associated in some groups, with the aecia. The evidence would seem to indicate that all the infection is primary. In one collection made in Wisconsin most of the infection on the leaves has resulted only in the development of aecia. Where infection occurred on the stems or capsules, telia are found associated with the aecia and in some cases only telia are present.

No heteroecious rusts have been recognized which have aecia on *Ludwigia*. Bisby (1916) has pointed out, however, that *P. Jussiaeae*, because of the character of its teliospores, is related, though specifically distinct, to a series of short-cycled forms on Onagraceae. The teliospores

of *Puccinia Jussiaeae* are of the same general type as those of *P. Peckii* (DeToni) Kellerm., a heter-eu-form having aecia on Onagraceae and uredinia and telia on *Carex*.

I should explain the situation as described in *P. Jussiaeae* as follows. An unconnected *Aecidium* exists on *Ludwigia* to which the name *Aecidium Ludwigiae* Ell. & Ev. should apply and to which most of the collections of aecia on *Ludwigia* should be assigned. This is quite certainly heteroecious though the connection has not yet been determined. The condition described as *Puccinia Jussiaeae* probably represents a transitional stage in the development of a micro-form from the aecia of the undetermined heter-eu-form. This parent eu-form would be expected to have teliospores like those of *P. Jussiaeae* and the diploid stage doubtless occurs on some genus of Poaceae or Cyperaceae.

One of the most interesting species in this series is *Uromyces coördinatus* Arth. This is an -opsis form occurring on *Euphorbia* (*Tithymalus*) *Palmeri* and *E. robusta* in the western United States. In common with those of many rusts on *Euphorbia*, the aecia develop from a systemic, perhaps perennial, mycelium which causes more or less distortion of the host. Telia occur more or less abundantly intermingled with the aecia, and teliospores are often to be found in the aecial cups. In some collections telia are fully as abundant as the aecia. Peridial cells and aeciospores like those of the aecia are abundant in these telial sori. The aecia of this -opsis form are like those of the heter-eu form *U. occidentalis* Diet. having uredinia and telia on species of *Lupinus*. The aecia of *U. occidentalis* occur on the same species of *Euphorbia* as does the -opsis form and also on *E. chamaesula*. They likewise have the same systemic habit as do the aecia of the -opsis form. There occurs on *E. robusta* and *E. chamaesula* also a micro-form, *Uromyces Tranzschelii* Syd., having the same habit. The teliospores of the three species of rust are essentially alike. *Uromyces coördinatus*, then, exhibits a transitional condition such as might arise in the formation of the micro-form *U. Tranzschelii* from the heter-eu-form *U. occidentalis*. Pycnia are known in all three species but seem to be absent in some collections of the micro-form.

Uromyces excavatus (DC.) Lév. as described by Tranzschel (1910) would seem to illustrate an exactly parallel case to that of *U. coördinatus* in the series of European species of rusts occurring on *Euphorbia* which have already been mentioned. It will be recalled that there are a number of rusts having systemic aecia on *Euphorbia*, with uredinia and telia on Fabaceae. Correlated with these are a series of micro-forms on *Euphorbia* which are also systemic. *U. excavatus* could be interpreted as a transitional

-opsis form which has appeared in the process of development of a micro-form from a heter-eu-form having aecia on *Euphorbia*.

Other examples illustrating the conditions brought out in the discussion of *P. microica*, *P. consimilis*, *P. gigantispora*, *P. opposita*, *P. Jussiaeae*, and *U. coördinatus* might be given, but these will serve the purpose of this discussion. All these forms are species more or less closely correlated with heteroecious eu-forms. All appear to exist in only one generation, the haploid, and all are best interpreted as transitional and perhaps temporary conditions arising in the formation of a micro- from a heteroecious eu-form in which the aecia of the parent long-cycled form continue to develop but have associated with them telia borne on the same (haploid) thallus. It should be emphasized that most of these forms show a tendency to omit the pycnia, perhaps in proportion to the relative abundance of telial development.

It will be noted that full support of the suggestion that -opsis forms may be derived from heteroecious eu-forms has not been found. Considerable evidence of the gradual formation of a micro-form from a heteroecious eu-form has, however, been presented which would seem to support the hypothesis previously made with reference to the origin of micro-forms.

These transitional forms are discussed here, however, as they have usually been considered to be of the -opsis type, and all the American species have been included in the genus *Allodus* or in *Pucciniola* of the Arthurian classification based on life histories (Arthur, 1906). It should be noted, however, that all the species mentioned appear to exist in but one generation only—the haploid. A true -opsis form must consist of two discontinuous generations as does a eu-form. The aecia of such a true -opsis form arise from basidiospore infection and are borne by the haploid generation. The aeciospores give rise to a diploid thallus bearing teliospores. It is pertinent to this discussion to raise the question as to whether it is to be expected that a true -opsis form would originate directly from a heteroecious eu-form. The aecia are borne on a separate host. In the eu-life cycle they are not capable of infecting that host but initiate the diploid thallus on the alternate host. In the transitional forms which have been mentioned, the normal thing to expect is that the aeciospores would continue in the usual manner to infect the alternate host so long as they remained functional. If, however, they should acquire the function of developing basidia, the basidiospores would then be expected to infect the aecial host, since that is the normal thing for basidiospores to do. Such an occurrence would presumably initiate an endo-form. If the aecia from which such an endo-form was derived developed on a mycelium of

local distribution in the host, the endo-form so derived would presumably be able to perpetuate itself only through that season and would not become permanently established unless the tendency is retained to develop teliospores in association with the endo-form. (See the discussion which follows of -opsis forms with repeating aecidia.) If on the other hand the aecial mycelium is perennial in the host, an endo-form initiated in this way would be able to perpetuate itself.

Origin of -opsis from aut-eu-forms

We may now turn our attention to the discussion of certain -opsis forms showing relation to autoecious eu-forms. Mention has already been made of the peculiar situation in *Puccinia Violae* as it occurs on *Viola glabella* and its probable relation to an -opsis form of the type of *P. effusa*. *Puccinia insperata* Jackson, occurring on *Nabalus hastatus* in Oregon and Alaska, is of interest in this connection. On May 16, 1915, the writer made the first collection of this species in the vicinity of Mount Hood in Oregon. The plants were quite young, and infection had occurred on the basal leaves. Aecia were abundant but no pycnia were observed with them. Telia accompanied the aecia in some cases. These occurred in such close relation that they were certainly borne on the same mycelium. When infection occurred on the petioles or involved a vein of the leaf the telia were more abundant. There was no evidence of scattered infection from aeciospores, and no urediniospores were observed in the telia. Had this collection been the only material available, the species would have been taken for an -opsis form. On July 24, 1915, however, I made another collection in the same spot and found abundant scattered uredinia and telia. The species has since been found in Alaska, and the collections from that region show the same condition as described for the Oregon material except that uredinia are not abundantly produced in proportion to the telia in collections made late in the season.

There are a number of species of *Uromyces* which show this condition. One of the most interesting for our purpose is *U. Suksdorfii* Diet. & Holw. This rust occurs on various species of *Silene* in western North America. Pycnia are unknown for the species. Two collections are especially interesting. Both were made in the early part of the season. One was made at Truckee, California, June 6, 1920, by E. Bethel and G. W. Posey and occurs on *Silene occidentalis*. This collection shows abundant infection resulting in aecia and closely associated telia on both leaf blades and petioles. Telia are more abundant in proportion to the aecia when infection occurs on the petioles. The other collection occurs on *Silene verecunda*,

and was made at Whitmore, California, by E. Bethel on June 26, 1923. This collection, while made early in the season, was on a more mature plant than the first. All the infection is evidently primary and consists of aecia with associated telia, except that on the youngest leaves a few spots show aecia only and on the oldest lower leaves as well as on the stems telia are produced exclusively. Infections on the leaves of intermediate age show aecia and telia closely associated, the latter often predominating. These two collections exhibit what has been considered a typical -opsis condition, and if taken alone they would be so interpreted. In fact, the latter collection was made the type of *Uromyces* (*Pucciniola*) *Betheli* Arth. However, Bethel made a second collection of the rust on the first host at the same locality (Truckee, California) July 23, 1922. This collection shows the same primary condition as the one collected in early June two years previously in a somewhat later stage of development and, in addition, a few scattered uredinia. Other collections of this species made later in the season show scattered uredinia and telia. It is noticeable, however, that uredinia are produced sparingly in proportion to the telia.

Uromyces Rikerianus Arth. occurs on *Rumex paucifolius* in the Rocky Mountain region. It was originally described with aecia and telia only. The type collection shows telia closely associated with the aecia, evidently from the same mycelium. The material available of this species is not abundant, but it clearly represents another case of a long-cycled form in which the early primary infection suggests an -opsis condition while the aeciospores give rise to a mycelium of limited growth which bears uredinia and telia. This species is the same as *Uromyces fuscatus* Arth., having all spore forms. It is of especial interest to note that pycnia have not yet been found in this species.

Uromyces Acetosae Schroet. as described and figured by Lindfors (1924) probably represents a similar case and is of special interest since Lindfors has given some interesting cytological data. *U. Acetosae* is ordinarily an aut–eu–form. According to Lindfors a form exists, however, which does not as a rule produce uredinia. This form has been made the basis of an independent species, *Uromyces borealis* Liro. The material studied occurred on *Rumex arifolius* and consisted of fully developed aecia and telia. Lindfors observed that telia were grouped closely around the aecial cups. A cytological examination revealed that the mycelium, consisting of uninucleate cells, from which the aecia arise, showed a wider distribution and continued frequently beneath the telia which are associated with the aecia. Lindfors was not able to demonstrate that fusion cells occur at the base of the telium but he felt convinced that some transition takes place

there from uninucleate to binucleate mycelium and that two forms of spores may thus appear after conjugation in this species on the same thallus. Unfortunately he does not mention whether pycnia are present or absent, and it is not made clear whether scattered uredinia and telia appear on these plants later in the season. The observation that the telia as well as the aecia with which they are associated develop from a mycellium which is prevailingly uninucleate is of importance, since it lends confirmation to the assumption made in the preceding discussion that such infections are primary and that the telia associated with the aecia are from the same mycelium.

Other examples of the condition shown in such aut-eu-forms as *Puccinia insperata*, *Uromyces Suksdorfii*, and *U. Rikerianus* might be cited. According to Morgenthaler (1910), *Uromyces Primulae* Fuck., *Puccinia Primulae* (DC) Duby, *P. Mulgedii* Syd., and *P. Lactucarum* Syd. behave similarly. *U. Primulae-integrifoliae* (DC.) Niessl. is apparently a transitional -opsis form correlated with *U. Primulae*. These illustrations are perhaps sufficient to emphasize the fact that aut-eu-forms are present in these genera which show an -opsis-like condition in the haploid generation but which develop the diploid generation in the usual way by the formation of scattered uredinia and telia. There are a number of species classed as true -opsis forms which exhibit this same condition except that the aeciospores give rise to a diploid mycelium which bears telia only. *Puccinia Carnegiana* Arth., *P. Podophylli* Schw., *P. intermixta* Peck, and *P. effusa* Diet. & Holw. may be mentioned as some of the -opsis forms which exhibit this condition.

It would appear that such -opsis forms might be derived from aut-eu-forms which exhibit the tendency illustrated above. It should be noted that the teliospores formed in association with the aecia in these eu-forms have a different history from those formed later in the season. The former have arisen directly on the haploid thallus. The latter have arisen on the diploid thallus which has resulted either directly from aeciospore infection or indirectly through urediniospore infection. Those teliospores formed on the haplont might be expected to give rise to another haplont bearing aecia and associated telia. The aeciospores of such a haplont have in turn a different history from those borne on a haplont originating from teliospores which were formed on the diplont, in that no aecia or uredinia have intervened. Such aeciospores then might exhibit a tendency to produce a diplont which would bear telia only. The accumulated tendency would perhaps tend to the development of a micro-form. If, however, the tendency to form aecia persisted, an -opsis form might arise by the gradual elim-

ination of the uredinial stage. Such an -opsis form might be developed parallel with the parent eu-form, and both might continue to exist. This might result if the tendency to the development of the -opsis condition appeared in one race of the parent form or on a particular host or in some isolated locality. If, however, the change took place in the eu-form simultaneously throughout its range, and the tendency to the immediate production of teliospores were strongly enough established, the original form might disappear and be replaced by the -opsis form.[10]

Species with repeating aecidia

There is another group of -opsis forms which deserve special mention. This group develops repeating aecidia. The first-formed mycelium from basidiospore infection presumably develops pycnia and aecia only. The aeciospores give rise to a localized mycelium from which other aecidia develop without accompanying pycnia. Associated with these secondary aecidia and arising from the same mycelium, telia are usually found in greater or less abundance. Aeciospores from the secondary aecia then give rise to other similar infections, and the process may be repeated several times during a season. Late infections are likely to develop telia only. Two of these forms have been studied cytologically and several of them have been studied experimentally. Dietel (1893, 1895) was perhaps the first to study these forms in culture. He determined that *Puccinia Senecionis* Lib., *P. commutata* Syd., *Uromyces Ervi* (Wallr.) Plowr., *U. Behenis* (DC.) Unger, and *U. Scrophulariae* (DC.) Fuck. possess repeating aecidia. Jordi (1904) has confirmed Dietel's results with *U. Ervi* and adds to the list *U. Hedysari-obscuri* (DC.) Wint. Bubák (1898) studied *Puccinia ambigua* (Alb. & Schw.) Lag. and showed that it also belongs to the series of forms which develop repeating aecidia. His results have been confirmed by Treboux (1912). In connection with these studies, Dietel has shown that primary infection from basidiospores of *Uromyces Scrophulariae* results in the development of pycnia and aecia only. The same results were obtained by Jordi for *U. Hedysari-obscuri*. Culture work with the other species has been with aecidiospores only.

Kursanov (1916) made a cytological examination of the primary in-

[10] The form of *Puccinia Violae* on *Viola glabella* previously mentioned would furnish an example of how an -opsis form like *P. effusa* may have arisen from it. In this case both the parent eu-form and the -opsis form persist. *P. effusa* in turn shows a tendency to develop a micro-form *Puccinia Podophylli* would serve as an example of an isolated -opsis form. No other rust is known with which it is correlated. The parent eu-form has presumably disappeared, but the -opsis form retains the tendency to develop telia on the haplont.

fection of *Uromyces Scrophulariae*.[11] He reports that such infections develop first pycnia, then aecidia, and a little later, on the same mycelium telia.

> The mycelium of this generation is made up principally of binucleate hyphae and in part of uninucleate hyphae. The spermagonia are almost exclusively composed of uninucleate hyphae, while the aecidia are formed of the two kinds of hyphae; one as prevalent as the other. Most of the aecidiospores are developed from binucleate hyphae which grow up from the lower part of the primordium and form bunches of short branches which are transformed directly into basal cells of the aecidiospores. Also in the same place and in fewer number the primary basal cells are developed resulting from an isogamic union of two neighboring fertile cells and forming, as the preceding ones, chains of aecidiospores. Finally the teleutospores are formed exclusively by binucleate hyphae.
>
> From aecidiospore infection the secondary generation is developed, consisting of aecidia and teleutospores, but no pycnia. In these cases, all the cells are naturally binucleate.
>
> Analogous phenomena have been observed in the primary and secondary generations of *Uromyces Behenis*. (Translation.)

It should be noted that Kursanov's observation of the occurrence of telia in association with the primary aecia does not accord with the results of Dietel.

It is thus established beyond reasonable doubt that some -opsis forms have developed in which the repeating spore form retains the morphology of the aecia. Evidence from herbarium specimens would indicate that there are other instances of this sort, among which may be mentioned *Puccinia tenuis* (Schw.) Burr., *P. Batesiana* Arth., *P. crassipes* B. & C., *P. araucana* Diet. & Neg., *P. Acnisti* Arth., *Uromyces oblongus* Vize, *U. Thaspi* (Opiz.) Bubák, *U. induratus* Syd. & Holw., and others.

The usual explanation of the life cycle in species of this sort would be that the basidiospores formed when the teliospores germinate give rise to a haploid thallus which bears pycnia and aecia. An aeciospore then gives rise to a diploid thallus which may develop teliospores in the normal way for an -opsis form or may give rise to a diploid thallus which bears aecidia associated with which telia may develop. The spores from these secondary aecidia give rise to a succession of diploid thalli in exactly the same fashion as would occur if uredinia were produced. This explanation admits a type of life history in a group of species, otherwise of reduced life cycle, which is without a parallel elsewhere in the rusts. To the writer it seems highly inprobable that the true explanation of this type of life cycle is as simple as this.

[11] This paper is in Russian with a French résumé. I have had available only the review in French by Kursanov (Bot. Cent. 135: 281. 1917).

It is unfortunate that no study seems to have been made of the germination of the aeciospores in any of these species. The only study of this sort which may have a bearing on the subject is that made by Barclay (1891). He records the results of very careful and thorough culture work and germination studies with *Uromyces Hobsoni* Vize (=*Uromyces Cunninghamianus* Barcl.), which occurs in India on *Jasminum grandiflorum*. This species as described by Barclay possesses aecia which develop in the normal way and produce aeciospores for a time. Later teliospores develop in the same cups. Infection from basidiospores developed from germinating teliospores results in the development of primary aecia which are accompanied by pycnia. Infection from aeciospores results in a secondary generation of aecidia which are not accompanied by pycnia. The teliospores are developed only in the aecial cups and occur in either generation. They germinate in the normal way with a four-celled basidium and four basidiospores. A study of the aeciospores, however, showed that they germinate by the production of a short promycelium-like tube which divides into two cells each of which develops a long sterigma-like projection, but no basidiospores are formed. According to Barclay the host is infected directly by the hypha-like sterigmata. The mode of germination, however, strongly suggests an endo-condition, as Barclay recognized.

Uromyces Hobsoni, as described, appears to differ from the type of rust just discussed only in that the teliospores are always found in the aecidial cups. The peculiar type of germination of the aeciospores in this species, when considered together with the method of origin of *Endophyllum*-like rusts previously discussed, strongly suggests that the development of repeating aecidia in this group of rusts is in some manner related to the endo-type of development.

In support of this viewpoint is the suggestion gained from a study of some of these rusts that their relationship is with heteroecious rather than with autoecious species. Correlations, are, however, not always clear. The teliospores of *Puccinia ambigua*, which occurs on *Galium*, are more nearly similar to those of *P. rubefaciens Johans.*, a micro-form on *Galium*, than to those of the autoecious *P. punctata* Link. Unconnected aecia of heteroecious species are also known on *Galium*.

P. commutata in the same way shows close relationship with *P. Valerianae* Cest., a micro-form. There are no long-cycled autoecious species of *Puccinia* on *Valeriana*. There is one aut-eu-*Uromyces*. An unconnected *Aecidium* (*A. Valerianellae* Biv.) is known on *Valerianella*, which resembles the aecia of *P. commutata* so closely that in America, at least, it was long confused with the latter. Of special significance, however, is the

close resemblance of the sori of *Endophyllum Valerianae-tuberosa and E. Centranthi-rubri* to the aecia of *P. commutata* and of the unconnected *Aecidium*.

Puccinia Senecionis occurs on *Senecio* sp. *Puccinia Senecionicola* Arth. is the only autoecious eu-form known to occur on members of the genus. It occurs in the American tropics and is clearly not related to *P. Senecionis*. All the other members of the Aecidiaceae occurring on this host genus are the aecia of heteroecious grass or sedge rusts or micro-forms of *Puccinia* amd *Uromyces* or are classed as -opsis forms. A number of unconnected aecia are also known.

With reference to *Vromyces Scrophulariae* the evidence of relationship with heteroecious rusts is especially interesting. No other rusts are recorded on the genus *Scrophularia*. An unconnected heteroecious *Aecidium* however, night easily be confused with the aecia of *U. Scrophulariae*. The only autoecious rusts known on members of the Scrophulariaceae are -opsis forms, with the possible exception of two unconnected uredo-forms in the tropics (which, of course, might represent the diploid phase of heteroecious species as in *P. Antirrhini* Diet. & Holw.). All the other rusts of this family are micro-forms, species of unconnected *Aecidium*, or the aecial stages of heteroecious forms.

Finally, with reference to *Uromyces Hobsoni*, it is of special interest that the only other rusts occurring on members of the Oleaceae are *Uromyces comedens* Syd., which occurs also on *Jasminum*, and is an -opsis form similar to *U. Hobsoni* in character; several unconnected (presumably heteroecious) species of *Aecidium* on various hosts, including *Jasminum*; three micro-forms of *Puccinia* on *Jasminum*, and the aecia of several heteroecious rusts including *Puccinia Chrysopogi* Barcl. with aecia on *Jasminum*.

The relationship of these forms, as indicated by the discussion above, strongly suggests that they have been derived from the haploid phase of heteroecious rusts. Further evidence might be furnished by a similar analysis of some of the other species which appear to have repeating aecia but which have not been studied in culture. It is, however, preferable to confine the discussion to those forms that have been proven to have repeating aecidia.

The aeciospores of heteroecious rusts do not normally attack the host on which they are borne. They are capable of infecting only the host which bears the diplont. It is on this account that the appearance of -opsis forms possessing repeating aecidia on the host which bears the haplont of a correlated heteroecious form assumes special significance and requires

explanation. It is hardly to be expected that -opsis forms of this type would develop from heteroecious species on the aecial host by the simple process of the aeciospores giving rise to a diplont which bears aecidia.

In the discussion of the origin of the genus *Endophyllum* evidence has been presented that the temperate-region species have been derived from the haploid phase of heteroecious species and that they continue to develop in each case on the aecial host. They are able to do this because the aeciospores have acquired the function of teliospores and germinate by the development of a basidium and basidiospores. It is quite to be expected that basidiospores would be capable of infecting the aecial host, since that is what the basidiospores of the parent species normally do.

In spite of the apparent lack of support furnished by Kursanov's (1916) cytological studies, it seems to the writer that in explaining the origin of -opsis forms possessing repeating aecidia from the haploid phase of heteroecious rusts it is necessary to assume that an endo-condition has intervened in order that the diplont may become established on the aecial host. In view of the facts that the thallus bearing the repeating aecidia does not appear to develop pycnia, that it often bears also telia in association with the aecidia, and that the aeciospores may apparently give rise to a thallus bearing teliospores only, it is evident that we are not dealing with an ordinary endo-type. There are a number of points that can be fully explained only after comprehensive cytological and detailed cultural studies of a number of species.

From our present knowledge of the variable nuclear history in microcyclic species in general and especially of the forms with binucleate mycelium, it would appear to be possible that an endo-condition might develop which, by extreme simplification in a direction opposite to that which has given rise to uninucleate forms, would finally result in an apparently diploid condition. The result would appear to be cases of diploid 'repeating aecidia' which because of their origin might be something fundamentally quite different (see Dodge 1929, p. 1759).

Forms of the type which have just been discussed may be interpreted for the present as arising from transitional -opsis forms, developed in the process of the origin of a micro-form from the aecial stage of a heter-eu-form, in which an endo-condition has arisen in the haploid generation, thus enabling the aecidia to develop successive generations on the host for the haplont. Such a species is in effect a combination of an endo- and a micro-form. It is of interest to note in this connection that such an endo-form, because resting teliospores are retained, may develop in temperate regions from aecia of heter-eu-forms which arise from a local mycelium.

Some of the species having repeating aecidia may also have arisen from autoecious forms in the same manner. It is possible that the other species which have been studied in culture, *Uromyces Ervi*, *U. Hedysari-obscuri*, and *U. Behenis* may have had such an origin, though it should be kept in mind that heteroecious rusts with aecia on Fabaceae are not unknown and that the great majority of rusts occurring on Caryophyllaceae are micro-forms or are the aecia of heteroecious species.

Typical -opsis forms

The foregoing discussion of the origin of -opsis forms has furnished no entirely satisfactory explanation of the origin of such typical species as *Puccinia claytoniata* (Schw.) Peck, *P. asperior* E. & E., *P. Jonesii* Peck, *P. Lindrothii* Syd., *Uromyces Psoraleae* Peck, *U. Argophyllae* Seym., or *U. porosus* (Peck) Jackson, all of which presumably develop pycnia with the aecia consistently and none of which shows any present tendency to the development of teliospores in connection with the haploid phase. In all these forms the aeciospores give rise to a diplont which bears telia only. It is, of course, possible that these forms have been derived from aut-eu-forms by the simple expedient of dropping the uredinial stage, but to the writer it seems highly improbable that their origin is to be explained by so simple a process. I should rather favor the idea that they have been derived in some manner from heter-eu-forms and occur on the aecial hosts of the parent species. This might be accomplished by the development of a temporary endo-condition which persisted long enough for the diplont to become established on the aecial host and which then disappeared. Forms with repeating aecidia may represent transitional conditions in the development of such typical -opsis forms from the parent heter-eu-form. Once the diplont is established on the aecial host, it is conceivable that the tendency to the development of the repeating aecidia might gradually disappear in some species.

I have already indicated how a micro-form may develop from an -opsis form as in *P. effusa*. There are many other cases of micro-forms correlated with -opsis forms. Of interest in this connection is the correlation shown between the typical -opsis *Uromyces Psoraleae* Peck and the micro-*Uromyces abbreviatus* Arth. The former occurs on *Psoralidium Purshii* and two other host species in this genus, while the latter occurs on the above-named host and on one other. *U. Psoraleae* is one of those -opsis forms which develop pycnia and aecia from a more or less systemic infection of the haploid generation. From the infection by the aeciospores, scattered telia which develop from a local, limited mycelium appear later in the

season. *U. abbreviatus* develops telia in association with pycnia from a systemic infection. The teliospores are like those of the -opsis form. A point of special interest is that in the telia of the micro-form may be found a few aeciospores and peridial cells which resemble those of the -opsis form. The evidence of relationship shown between these species is strongly suggestive that in *U. abbreviatus* we have an example of a micro-form developed from the haploid generation of *U. Psoraleae*, an isolated -opsis form, or perhaps an example of an -opsis and a micro-form both developed from a previously existing heteroecious form with aecia on *Psoralidium*.

Heteroecious -opsis forms

The discussion of -opsis forms would not be complete without special mention of *Gymnosporangium* and *Calyptospora*. These genera are both heteroecious and, with a single known exception (*Puccinia interveniens* (Peck) Bethel), include all the heter-opsis rusts known at the present time. In the genus *Gymnosporangium* only one species, *G. nootkatensis* (Trel.) Arth., is known which bears urediniospores. This species is also one of the three or four members of the genus which develop cupulate aecia. It would appear that the primitive forms of this genus bore uredinia and cupulate aecia. The loss of the uredinia in *Gymnosporangium* and doubtless also in *Calyptospora* has presumably been associated with the fact that in these genera the diploid phase is perennial or normally overwinters as mycelium. The development of this habit in the diplont has apparently resulted in the dropping out of the diploid conidial stage. The perennial habit is not uncommon in the haplonts of heteroecious rusts and in the micro-forms derived from them, but is comparatively rare in the diplonts. It occurs in a few other forms as, for example, in *Melampsorella elatina* (Alb. & Schw.) Arth., *Chrysomyxa Pyrolae* (DC.) Rostr., and in some species of *Hyalopsora*, but *Calyptospora* and *Gymnosporangium* are the only genera known in which this habit is characteristic.[12]

The -opsis forms, in general, appear to be a heterogeneous group which have been derived in various ways from eu-forms. Some of them probably represent merely transitional conditions in the development of micro-forms. An analysis of the evidence presented in the foregoing discussion strongly supports the preliminary hypothesis that the forms of -opsis life history have not in general originated by the simple process of the uredinial stage being dropped in a eu-form, but that they have been derived in

[12] Such forms should not be confused with brachy-forms of the type of *Uromyces Glycyrrhizae*, *Puccinia suaveolens*, and *Trachyspora Alchemillae*, which are to be discussed in the next section.

various ways from the parent eu-forms by a change which is first expressed in the haploid generation of the latter. *Gymnosporangium* and *Calyptospora* are apparently exceptions.

THE ORIGIN OF BRACHY-FORMS

The brachy-forms, those which develop pycnia, uredinia, and telia, may be quite simply derived from autoecious rusts. One has only to study species such as *P. Orbicula* to obtain a complete picture of the probable origin of this type of rust. The situation in this species has been reviewed in some detail in the early part of this paper and mention has also been made of the culture work with *P. Helianthi* and *P. punctata*.

A study of the phenomena exhibited by such species suggests the hypothesis that the brachy-forms have been derived simply by the development of a sorus of urediniospores instead of an aecidium on the haploid mycelium as the first spore form following the initiation of the diploid phase. The aecidium would thus be eliminated, its place being taken by a primary uredinium or uredinoid aecium. Judging from the situation found in the species mentioned above, the process may be a gradual one, both types of life cycle apparently continuing through many generations.

The usual test for a true brachy-form has been the finding of pycnia associated with primary uredinia. Species of rusts for which only uredinia and telia are known have been classed as hemi-forms. These have usually been assumed to be the diploid generations of heteroecious species whose aecial connection has not been established, or autoecious species whose aecia have not yet been discovered. Some of these are doubtless also brachy-forms whose primary uredinia have not yet been observed. The work of Kursanov (1922) and Lindfors (1924) on *Trachyspora Alchemillae* (Pers.) Fckl., reviewed below, suggests that brachy-forms may exist in which pycnia do not appear in association with the primary uredinia. They showed in that species, which is not known to develop pycnia, that a haploid mycelium occurs in a primary infection.

Cytological studies of brachy-forms have not been numerous. *Phragmidium* (*Frommea*) *Potentillae-canadensis* Diet. was studied by Christman (1907b). *Triphragmium Ulmariae* (Schum.) Link has been studied by Olive (1908), Kursanov (1922), and Lindfors (1924). Both species have the usual nuclear cycle so far as they have been studied. Kursanov and Lindfors have also examined *Trachyspora Alchemillae*. This species develops the primary stage from a perennial mycelium, and a vegetative mycelium of both uninucleate and binucleate cells is present according to Kursanov. The two authors do not agree as to the details. Lindfors holds

that all the mycelium is to be interpreted as uninucleate and that the urediniospores are all primary, the binucleate condition arising through fusion of cells or migration of nuclei. Kursanov agrees that some of the urediniospores originate in this way, but concludes that the majority are formed directly from the binucleate mycelium and are secondary. He apparently thinks that the perennial mycelium is made up of independent haploid and diploid thalli, thus agreeing with Olive's (1913) explanation of *Puccinia Podophylli*, *P. suaveolens* (Pers.) Rostr., and *Uromyces Glycyrrhizae* (Rab.) Magn. Lindfors found that teliospores are frequently produced in later stages of the primary uredinia. He apparently considers that they are developed in the same way as the urediniospores from fusion cells. The urediniospores developed from primary infections in such brachy-forms give rise to a scattered infection of uredinia and telia which develop from a mycelium of limited growth.

No brachy-forms of *Puccinia* or *Uromyces* have been studied cytologically with the exception of *Uromyces Glycyrrhizae* and *Puccinia suaveolens*. The former was studied by Olive (1913), the latter by Olive (1913) and Kursanov (1922). In both these species the initial stages develop from a perennial or at least from a systemic infection, and the cytological study has revealed certain very puzzling features as to the nuclear history which have never been satisfactorily explained. Both these species develop a localized diploid phase from primary urediniospore infection. It would not appear to be necessary to review the results of these studies at this time except to point out that a peculiar intermingling of haploid and diploid mycelia has been found in the systemic infections.

As noted above, all brachy-forms may apparently be derived from autoecious rusts by the production of uredinia as the first spore form on the haplont instead of aecidia. Most of the brachy-forms develop a haplont of limited growth. Such forms are to be derived from aut-eu-forms in which the aecia develop from a limited mycelium. Should a brachy-form develop, however, from an aut-eu-form whose haplont was perennial or systemic in the host, and whose diplont developed from a scattered and localized infection, every condition would be present for the appearance of such forms as *Trachyspora Alchemillae*, *Uromyces Glycyrrhizae* and *Puccinia suaveolens*. According to my interpretation, then, these three brachy-forms and others of like habit have probably been derived from aut-eu-forms whose haploid phase was perennial or systemic. Of interest in this connection is the fact that there exists a short-cycled form, *Trachysporella melospora* (Therry) Syd. on *Alchemilla* spp., the teliospores of which resemble those of *Trachyspora Alchemillae*. The telia of the micro-

form develop from a systemic infection. The general habit of the species is much like that of the primary uredinia of the brachy-form.

In the process of formation of a brachy-form from an aut-eu-form whose haplont was perennial or systemic, it is not surprising that an apparently anomalous nuclear history should appear in the derived form. When it is possible to compare the cytological details found in such derived forms with those which doubtless occur in a transitional form of the type of *P. Orbicula*, all of whose sori develop from limited mycelium, a basis will be furnished for a proper interpretation of the nuclear phenomena, and we shall probably not need the elaborate, though apparently strictly orthodox, explanation of an independent and simultaneous occurrence of haplont and diplont in the same plant as put forward by Olive and Kursanov to explain their findings.

It is worthy of mention that the brachy-forms appear to be a group of comparatively recent origin. There are no known rusts having this type of life history in the Uredinaceae (Melampsoraceae) (*Kuehneola* and *Spirechina* are clearly related to the tribe Phragmidiatae). Brachy-forms occur only on members of the dicotyledons and are rare on the more primitive orders. Such as do occur on primitive orders appear to belong mainly to the Phragmidiatae or Uropyxidatae. Eighty per cent of the brachy-forms occurring in North America on members of the Archichlamydeae occur on the Leguminosae and Rosales, the two orders in that group which also bear the largest number of aut-eu-forms. By far the larger number of the brachy-forms on Leguminosae belong to the Raveneliatae. Brachy-forms, particularly in *Puccinia* and *Uromyces*, reach their culmination on the Metachlamydeae. Of the sixty-six North American species assigned to the genus *Bullaria* (brachy-*Puccinia*), nineteen species occur on the Archichlamydeae, all of these on the more modern orders, which with the exception of five which occur on Umbelliflorae, are subtropical. Thirty-seven of the sixty-six species occur on the Asterales (see table 9, pp. 86–87).

The tendency which *P. Orbicula* shows to the development of a micro-form has already been mentioned. It will be recalled that teliospores are not uncommonly developed in the primary uredinia of this rust. Kursanov (1922) has mentioned the appearance of teliospores in the primary uredinia of *Triphragmium Ulmariae*. The close correlation shown between the brachy-form *Uromyces bidenticola* (P. Henn.) Arth. and the micro-form *Uromyces Bidentis* Lagerh. is also of interest. These observations together with several other correlations similar to the one just mentioned lead to the conclusion that some micro-forms may be derived from

brachy-forms by the accumulation of the tendency to form teliospores in the primary uredinia. In this way the secondary uredinial stage would be gradually eliminated and a micro-form would result. It is probable that the origin of a considerable number of the micro-forms derived from autoecious rusts may be accounted for by this method.

Finally it should be emphasized that, in common with the other types of life history already discussed, the brachy-forms are to be derived from the eu-forms through a change which is first expressed in the spore form developed on the haploid thallus.

SUMMARY AND DISCUSSION OF THE ORIGIN OF LIFE CYCLES

A brief summary may now be furnished of some of the more important points of the hypotheses which have been presented to explain the origin of the various types of life cycle as brought out in the foregoing detailed discussion.

The micro- (including the lepto-) forms are to be derived in various ways. The great majority have apparently arisen from the haploid generation of heteroecious eu-forms, telia finally completely replacing the aecia. Some have probably been derived through an -opsis condition which develops in certain aut-eu-forms, while others have developed from autoecious rusts through the brachy-forms.

The endo-forms, so far as they are known, may all be derived from the aecidial stage of heteroecious-eu-forms, with the single exception of *Kunkelia nitens* which probably developed from the caeomoid aecial stage of an aut -opsis form. There would seem to be no reason, however, why an endo-form should not develop from the aecial stage in any type of life cycle. The endo-forms represent, then, merely a special simplified life history type comparable to the micro-forms in which the fusion of the paired nuclei typically takes place in the first spore form developed on the haploid thallus.

The -opsis forms in considerable part probably represent merely transitional stages in the process of the gradual development of micro-forms from either heter- or aut-eu-forms. Those with repeating aecidia exhibit a special type of life history which has presumably developed in the process of the origin of a micro-form from a heter-eu-form by the development of an endo- tendency in the aecia. The method of development of some true -opsis forms cannot be traced exactly, but they may have originated from the haploid phase of heteroecious species possibly through forms having repeating aecidia. The heter-opsis forms are perhaps derived by the simple dropping of the uredinia from the life history.

The brachy-forms are all to be derived from aut-eu-forms by the appearance of urediniospores as the first spore form in primary infections instead of aecidiospores.

The general tendency seems to be directed toward the production of a micro- or endo-form, in either of which the two essential points in the rust life cycle are brought as close together as possible on the haploid thallus. The relationship and origin of the various types of life cycles may be illustrated diagrammatically. Such a diagram is shown in figure 1, on page 94.

In deriving all these types of life history from those of longer life cycle the fact has been stressed that they seem to have their origin in a change which is first expressed in the spore form developed on the haploid thallus. This may perhaps be better stated by saying that in the regressive development from the longer to the shorter type of life cycle the haplont has survived and the diplont has gradually become shortened and finally practically eliminated (completely so in uninucleate forms). The process of shortening of the life cycle as it has been traced in the preceding pages, and the persistence of the haplont serve to direct attention to the fundamental importance of the aecium in the long-cycled parent forms as a 'sexual' apparatus and strengthens the arguments of those who have held that the fusion of cells or migration of nuclei as it occurs in the rusts is the survival of a real sexual process.

While the change which results in a shortening of the life cycle seems, in most cases, to originate in the haplont and the diplont is commonly shortened, as noted above, it should be recognized that in many cases, as in the micro-forms having binucleate mycelium throughout, it is the diplont which has survived. Dodge (1919, p. 1758) has also presented evidence that at least one uninucleate form may be best interpreted as having diploid nuclei.

It will be observed that nearly all the argument presented in this paper is based on the rusts of temperate regions and that tropical species are rarely cited. This is necessary because of our incomplete knowledge of tropical rusts particularly with reference to heteroecism. One of the noticeable features of tropical rusts, however, is the considerable number of odd microcyclic forms which are apparently not closely related to any of the present temperate-region groups, and which in many cases are not closely related to any other tropical rusts. I refer to such genera as *Dietelia*, *Pucciniosira*, *Alveolaria*, *Masseeela*, *Beodromus*, *Trichopsora*, *Didymopsora*, *Gambleola*, *Botryorhiza*, *Endophylloides*, *Coleopuccinia*, *and Gopania*. With the exception of the last four these genera are included by Dietel (1928) in the sub-family Pucciniosirae of the Pucciniaceae.

There is considerable evidence that evolution in the rusts has proceeded more rapidly in the tropics than in temperate regions, and such genera may in part be interpreted as representing the end products of lines of development which have taken a course similar to that which has been discussed; the original heteroecious form, together with the intervening autoecious eu-, brachy-, and -opsis forms, having in many cases disappeared.

If this reasoning is sound, the further suggestion may be made that the parasitic Auriculariales, at least those occurring on bryophytes and pteridophytes, such as *Jola* and *Eocronartium*, and perhaps also the Ustilaginales, may represent micro-forms which are the end products of a regressive development, similar to that now taking place in the rusts, which has occurred in rust-like ancestors. This suggestion would be in line with the opinions of those who would derive these orders from the same ancestral line as the rusts (Linder, 1929).

It should be recognized, however, that, after becoming microcyclic, it is possible that some rusts may have undergone some further modification in morphology. It is conceivable for example that from *Endophyllum*, or from endo-forms derived from aecia other than *Aecidium*, a group of microcyclic forms may have developed through lateral adherence of the chains of spores and the loss or alteration of the peridium, resulting in such genera as *Dietelia*, *Endophylloides*, *Pucciniosira*, *Gambleola*, *Didymopsora*, and *Trichopsora*.

Contributing evidence in support of the suggestion made in the last paragraph has been obtained by an examination of *Gambleola cornuta* Massee and *Trichopsora Tournefortiae* Lagerh. In *Gambleola* the two-celled teliospores are formed in chains and adhere closely both laterally and vertically to form a long hair-like column. A careful examination of the structure of these columns of teliospores reveals that each two-celled spore is separated by a distinct intercalary cell and that there is a delicate but evident peridium present which apparently covers the entire column of spores. These morphological points appear not to have previously been noted in this genus. In *Trichopsora*, the hair-like columns of spores adhere because of the gelatinization of the cell wall. In this genus the spores germinate by the division of the contents into four cells as in *Coleosporium*. While no detailed study of the development of the sori has yet been made, it is quite evident that the spores are formed in chains as in other genera of this type. A study of crushed mounts of spore columns stained with cotton blue in lacto-phenol, reveals the presence among the spores of additional narrow, elongated binucleate cells, also with gelatinous cell

walls (the 'sterilen Zellen' of Lagerheim, 1891, p. 348). These narrow cells, which are about one fourth the diameter of the spores, appear to be connected with the spores by greatly elongated extensions of the gelatinous cell wall. Their presence may be demonstrated even after the spores have germinated by the deeply stained contents. The writer would interpret these extra cells as intercalary cells. No evidence of a peridium was found.

In *Didymopsora* and *Pucciniosira* intercalary cells occur, at least in some species, and in the latter genus an evident peridium is present. These two genera, as well as *Gambleola* and *Trichopsora*, are in all the essential features of their morphology very much like *Endophyllum* except in the character of the spores. It seems quite possible that their origin may be similar to that of *Endophyllum*. It also appears reasonable to expect that a detailed study of other tropical microcyclic genera would reveal the presence of intercalary cells. If it is conceivable that in some forms the intercalary cell might function as a spore, still other genera of short-cycled forms might be brought into line with this suggestion. It is possible that the report by Arthur and Fromme (1915) that in *Endophyllum tuberculatum* two-celled spores are not uncommon may be interpreted as evidence in support of this suggestion (see also Arthur, 1929, fig. 139). The details of their formation are, however, unknown. Dodge (1929, p. 1762) reports that in an American form of *Endophyllum Sempervivi* two-celled spores may be formed by the persistence and enlargement of the intercalary cell which remains intimately associated with the adjoining spore cell. One of the greatest needs in the development of our knowledge of the rusts, is detailed studies of the development and nuclear history of these odd microcyclic forms.

THE ANTIQUITY OF HETEROECISM

It will be observed that in the discussion of the origin of the various types of reduced life cycle the conclusion is reached that the great majority of such forms are probably derived from heteroecious rusts. The evidence of relationship as shown by correlation and by the close correspondence in hosts is often very striking. In only a few cases are these forms to be derived from autoecious rusts. The brachy-forms, to be sure, probably are all so derived, but, as previously noted, these forms as a group are quite certainly of recent origin. In general the discussion with reference to the various types of life cycle which has been presented in the preceding pages suggests strongly that heteroecism may be a primitive character in the rusts, and on this account it seems necessary to review the available evidence bearing on this subject.

The evidence to be obtained from an examination of the character of the rusts which occur on the different groups and families of host plants will first be presented.

All the rusts occurring on gymnosperms are stages of heteroecious species with the exception of *Gymnosporangium bermudianum* (an aut-opsis form) and of a few micro-forms, such as *Coleosporium* (*Gallowaya*) *pinicola*, *Chrysomyxa Abietis*, *C. Weirii*, *Melampsora* (*Necium*) *Farlowii*, and the repeating gall-forming endo-Peridermiums. According to the interpretation of the writer based on the evidence given in the preceding pages, these micro- and endo- forms are all to be derived from the haploid generation of heter-eu-forms. The -opsis *Gymnosporangium* is also presumably so derived, and will be mentioned again. It may be said, then, that all the rusts on gymnosperms are stages of heteroecious species or microcyclic forms probably derived from such species. There are no aut-eu-forms known on this group of hosts. All the long-cycled species occurring on the Abieteae are the aecial stages of species of *Coleosporium*, *Cronartium*, *Chrysomyxa*, *Pucciniastrum*, *Melampsora*, *Melampsorella*, *Uredinopsis*, *Hyalopsora*, *Milesia*, *etc.* All the rusts on the Cupresseae are the diploid stages of heteroecious species of *Gymnosporangium* (except the aut-opsis *G. bermudianum*).

All the rusts occurring on pteridophytes whose life histories are known are the diploid stages of heteroecious species whose aecia occur on members of the Abieteae (*Abies* and *Tsuga*). Of those whose life history is not fully known there is no evidence that they are not also heteroecious (Arthur, 1924). It may be emphasized at this time that the heteroecious genera to which the aecia occurring on Abieteae belong are among those rusts which have been considered the most ancient (Arthur, 1924; Faull, 1929).

The objection might be raised that the present species of gymnosperms and pteridophytes on which rusts now occur are modern species and that they may have evolved considerably later than some of the species in other families of plants which are also hosts for rusts. On this account it seems desirable to review the rust floras of some of the orders of angiosperms which are considered to be primitive.

On the order Magnoliales, which many modern students consider to represent one of the most primitive of angiosperms, there is but one known species of rust, *Goplania Micheliae* Rac. which occurs on *Michelia velutina* in Java. This rust is perhaps best interpreted as a very reduced and special type of derived micro-form. Two other species have been referred to this rust genus, both of which occur on other unrelated orders of hosts. No pycnia are described for any of them.

On the members of the order Anonales there are several unconnected aecidial forms, presumably the aecia of heteroecious rusts, one little-known species of *Puccinia* which is apparently an -opsis form, one unconnected species of *Uredo* (which may belong to the diploid phase of a heteroecious species), the type of the very interesting monotypic genus *Dasyspora*, *D. gregaria* (Kuntze) P. Henn. on *Xylopia*, which is a brachy-form with externally developed hyphoid uredinia, and *Sphaerophragmium Chevalieri* Har. & Pat., presumably a brachy-form, though uredinia are undescribed.

The members of the family Lauraceae, order Laurales, bear several unconnected aecidial forms, one unconnected *Uredo*, and the only known species of the genus *Xenostele*, *X. Litseae* (Pat.) Syd. and *X. Echinaceae* (Berk.) Syd., which are certainly to be interpreted as special types of microcyclic forms, probably derived. On the related Monomiaceae there is one unconnected *Aecidium*.

The rusts on members of the Ranales form an interesting series. By far the great majority of species occur on *Anemone* and *Ranunculus*, or on genera closely allied. On *Anemone* there occur a considerable number of species of *Aecidium*, for several of which the connection with heteroecious rusts is known, several micro- and -opsis forms of *Puccinia*, and one aut-eu-*Tranzschelia*, which is clearly correlated through *T. fusca* and *T. tucsonensis* to the heter-eu- *Tranzschelia punctata*. On *Ranunculus* all the rusts are micro-forms of *Puccinia* or aecial forms, connected or isolated, together with one -opsis and one micro-*Uromyces*. On *Caltha* there are three aut-eu-forms and two micro-forms of *Puccinia*. On the other genera the rusts are all aecial forms of heteroecious species or unconnected aecia, or micro-forms of *Puccinia* with the exception of one -opsis *Uromyces* and one micro-*Triphragmium* on *Isopyrum*. To these should be added the diplonts of eight species of *Coleosporium* and one *Cronartium* and one or two hemi-forms of *Puccinia* and *Uromyces*, which may be either aut-eu-forms or the diploid phases of heteroecious species.

On the family Berberidaceae there are a number of unconnected aecial forms, also several known to be the aecial stages of heteroecious rusts, several micro-forms of *Puccinia*, two -opsis forms (including *P. Podophylli*), and three or more hemi-forms of *Puccinia* usually referred to *Uropyxis*, a genus assumed to include only brachy-forms. To these should be added the type of the monotypic genus *Gambleola*, *G. cornuti* Mass., which is obviously a special type of microcyclic form probably derived. On the related Menispermaceae there is one doubtful unconnected *Aecidium* and one hemi-*Uromyces*.

On members of the Aristolochiales there occur one aut-eu- and one micro-*Puccinia*. On members of the order Piperales there are two unconnected tropical *Uredo* forms, which may well be the diploid phases of heteroecious rusts. On the Rhoeadales, including the Papaveraceae and Fumariaceae, there are four species of *Aecidium*; two of these are unconnected, one is the aecial stage of a poaceous *Puccinia*, and the other is the aecial stage of *Cerotelium Dicentrae* (Trel.) Mains & Anders. In addition there are one micro-*Puccinia* and the aecial stage of one species of *Melampsora*.

The only rusts on the Loasales are diploid stages of two heteroecious species, one *Cronartium* and one *Coleosporium*, together with an aecial form assigned to the heteroecious *P. subnitens*, and one unconnected *Uredo*, which may well be the diploid stage of a heteroecious species. On the Capparidales are one unconnected aecial form and one assigned as the aecial stage of *P. subnitens* Diet., together with one unconnected *Uredo*. To these should be added *Hemileia Schefferi* Syd., a doubtful hemi-form, and the very interesting isolated micro-form *Masseeella Capparidis* (Hobs.) Diet.

On the Cruciales the rusts are all either unconnected aecial forms or the aecial stages of heter-eu-*Puccinia* or derived micro- and -opsis forms of *Puccinia*, together with one somewhat doubtful micro-*Uromyces*.

On the members of the Violales there are two species of aut-eu-*Puccinia*, two -opsis forms of *Puccinia*, and three micro-forms. A number of aecidia also occur which are the aecial stages of heteroecious species of *Puccinia* or *Uromyces*. There are also one caeomoid aecial stage of a *Melampsora* and one unconnected *Uredo* which suggests relationship with the Pucciniastrae and is probably the diplont of a heteroecious species.

There occur on the Polygalales one unconnected *Uredo*, several unconnected aecia, and one micro-*Puccinia*, together with two hemi-forms; one each in *Uromyces* and *Puccinia*.

On the Crassulaceae of the Saxifragales there occur one unconnected *Aecidium*, several aecidia whose connection with heteroecious species is known, a number of species of micro-*Puccinia*, one *Endophyllum*, and one unconnected *Uredo*. On the Saxifragaceae there are two aecial stages for heteroecious species of *Melampsora*, together with two autoecious species of *Melampsora* and the diploid phase of one species of *Coleosporium* and of two in *Cronartium*. Of the Aecidiaceae there are one rare tropical hemi-*Puccinia* on *Montinia*, one *Endophyllum* and two species of *Pucciniostele* on *Astilbe*, both -opsis forms. The other rusts on members of this family are all aecia of heteroecious species of *Puccinia* or are micro-forms. There are no species of *Uromyces*.

With the exception of the diploid phase of *Melampsorella elatina*, all the rusts on the Caryophyllales are members of the Aecidiaceae. On the members of the family Portulacaceae there are two unconnected species of *Aecidium*, three -opsis *Uromyces*, one -opsis *Puccinia*, and one micro-*Puccinia*. On the members of the family Caryophyllaceae there are two unconnected forms of *Aecidium* and one of *Uredo*. Of the species of full life history in *Puccinia* there is but one known aut-eu-form (*P. Silenes* Schroet.). Two or three hemi-forms occur which may be diplonts of heteroecious species. There are several micro-forms. In *Uromyces* there are two or three aut-eu-forms and one certainly known heteroecious species with aecia on *Euphorbia*. Several hemi-forms occur which may have a similar life history to the last-mentioned. There is one -opsis form with repeating aecia (*U. Behenis* (DC.) Unger). On the Aizoaceae there are an aecial form assigned to *P. subnitens*, one aut-eu-*Puccinia*, one -opsis *Puccinia*, and one hemi-*Puccinia*.

The rusts on the Polygonales form an interesting series. The only mem ber of the Melampsoraceae occurring on this order is *Phakopsora alpina* (Schroet.) Arth. This genus is presumably heteroecious, and the diplont of the species mentioned occurs on *Rumex alpina*. Dietel (1928) includes this species in *Schroetariaster* in the Pucciniacese. With the possible exception of one or two species of *Uredo*, the other rusts occurring on this order are members of the Aecidiaceae. There are three species of unconnected *Aecidium*. At least two heteroecious species of *Puccinia* are known which have the haploid phase on Polygonaceae (*P. rubella* (Pers.) Arth. and *P. subnitens* Diet.). A number (12+) of species of *Puccinia* are known only in the diploid phase (hemi-forms). At least four species are known which are heteroecious with their haploid phase on Umbelliflorae or Geraniaceae. Many of the hemi-forms probably have a similar life history. There are several micro-forms but no known species of aut-eu-*Puccinia*. The only certain autoecious rusts in this family are six species of *Uromyces*. In this genus there is also one known heteroecious form with the diplont on Polygonaceae (*U. Rumicis*). The other known species of *Uromyces* are hemi-forms. In addition there are four or more unconnected species of *Uredo*.

On the members of the order Chenopodiales, including the families Chenopodiaceae and Amaranthaceae,all the rusts are apparently included in *Puccinia* and *Uromyces* except perhaps some of the unconnected *Uredo*-forms. There are six aut-eu forms, several hemi-forms and species of unconnected *Uredo*. There are also seven species of *Aecidium* which are unconnected and at least four others which are known to be the aecial

stages of heteroecious species. Six micro-forms are known together with three -opsis forms of *Uromyces*.

This review might be considerably extended. The brief analysis of the rusts occurring on members of the 17 above-mentioned orders will perhaps be sufficient to bring out forcibly the fact that the great majority of the rusts on the more primitive families of angiosperms are heteroecious or are -opsis and micro-forms presumably derived. In this review an attempt has been made to include all the rusts known to occur on the orders mentioned. It is admittedly difficult to do this with absolute accuracy because of the scattered literature. On this account a tabulation (table 9) of the rust species occurring in North America, based on the North American Flora, has been prepared, in which all the rusts have been arranged by orders of their host plants. For convenience the arrangement of orders in the dicotyledons follows that of Hutchinson (1926), which was also followed in selecting the orders discussed above. The arrangement of the monocotyledons follows that of Engler and Prantl. In table 9, haploid and diploid phases of heteroecious species have been listed separately. The unconnected aecidial forms are also listed separately, though it is probable that nearly all of these are haploid phases of heteroecious species. The uncertain diplonts, hemi-forms, and unconnected species of *Uredo* are combined in the last column. Some of these are probably aut-eu-forms, others brachy-forms, though a considerable number, especially of unconnected species of *Uredo*, are probably diplonts of heteroecious species. The figure to the left in each column refers to the number of species of the Uredinaceae while that to the right gives the number of species referred to the Aecidiaceae.

If we consider, then, for the sake of greater accuracy, only the North American rusts occurring on the orders enumerated in the preceding paragraphs (the first 17 in table 9) it may be said that out of a total of 148 species, 50 are either haploid or diploid stages of heteroecious rusts, and 56 are endo-, micro-, or -opsis forms. Some of the hemi-forms and those known only in the uredinial stage are quite certainly diplonts of heteroecious species. There are only 12 species certainly known to be aut-eu-forms and only four brachy-forms, three of which are included in *Uropyxis* and one in *Dasyspora*.

In this connection the general distribution of long-cycled autoecious forms is of considerable interest, not only with reference to the host families on which they occur but also with reference to their distribution among the various families and subfamilies of the rusts.

No aut-eu-forms are known on gymnosperms or pteridophytes. All the

TABLE 9

Numerical distribution of North American rusts among the orders of the hosts according to the life history of the parasite

	HETEROECIOUS HAPLONTS	HETEROECIOUS DIPLONTS	MICRO-FORMS	ENDO-FORMS	AUT-OPSIS FORMS	UNCONNECTED AECIDIA	AUTOECIOUS EU-FORMS	BRACHY-FORMS	HEMI-FORMS AND UREDO
PTERIDOPHYTA	..	16—1	..	..	..	..	..	..	..
GYMNOSPERMAE	48—	—27	3—	3—	— 1	8—	..	..	..
ANGIOSPERMAE	..	..	..	..	..	..	..	..	..
ARCHICHLAMYDEAE	..	..	..	..	..	..	..	..	..
Magnoliales	..	..	..	..	..	..	..	..	..
Anonales	..	..	..	..	..	— 1	..	— 1	— 1
Laurales	..	..	..	..	..	..	..	..	..
Ranales	— 9	..	—11	..	— 5	— 1	— 4	..	— 2
Berberidales	— 4	..	— 1	..	— 1	— 1	..	— 3	..
Aristolochiales	..	..	— 1	..	..	..	..	..	..
Piperales	..	..	..	..	..	..	..	..	— 1
Rhoeadales	1— 1	..	— 1	..	..	— 1	..	..	..
Loasales	— 1	1—	..	..	..	..	..	..	— 1
Capparidales	— 1	..	..	..	..	..	..	..	..
Cruciales	— 2	..	— 7	..	— 1	..	..	..	..
Violales	— 2	..	— 3	..	— 1	..	— 1	..	..
Polygalales	..	..	— 1	..	..	— 1	..	..	— 2
Saxifragales	1— 1	..	—10	—1	..	— 1	..	..	..
Caryophyllales	— 2	1— 1	— 4	..	— 4	..	— 1	..	— 3
Polygonales	— 5	— 6	— 1	..	..	— 1	— 3	..	— 7
Chenopodiales	— 4	..	— 1	..	— 2	..	— 3	..	— 9
Geraniales	— 4	— 2	— 1	..	..	— 1	1— 1	..	— 1
Lythrales	— 4	1—	— 6	..	— 1	— 2	— 3	..	— 3
Thymelaeales	— 1	..	..	..	..	— 3	..	..	..
Dilleniales	..	..	— 1	..	..	..	..	..	— 1
Bixales	..	..	..	..	..	..	..	..	— 2
Passiflorales	— 1	..	..	..	..	..	..	..	..
Cucurbitales	..	1—	..	..	..	..	..	..	— 1
Cactales	..	..	..	..	..	..	..	..	— 1
Myrtales	..	..	..	..	..	..	..	..	— 2
Guttiferales	..	..	..	..	..	..	— 1	..	— 1
Tiliales	..	..	1— 2	..	..	— 1	..	..	..
Malvales	— 2	1—	— 7	— 1	..	..	..	— 1	..
Malpighiales	..	1—	..	..	..	— 1	— 1	— 4	— 3
Euphorbiales	— 6	3—	— 1	..	— 2	— 6	5— 3	— 3	— 5
Cunoniales	1— 3	4—	— 2	..	..	..	..	..	..
Rosales	—24	4—	— 3	— 1	— 6	..	—16	—11	— 1

TABLE 9 (Continued)

	HETEROECIOUS HAPLONTS	HETEROECIOUS DIPLONTS	MICRO-FORMS	ENDO-FORMS	AUT-OPSIS FORMS	UNCONNECTED AECIDIA	AUTOECIOUS EU-FORMS	BRACHY-FORMS	HEMI-FORMS AND UREDO
Leguminosae	..	2— 3	—10	..	1— 10	— 2	—10	—68	—25
Salicales	..	8—	..	..	..	..	..	..	..
Myricales	— 1	1—	..	..	..	..	..	..	..
Fagales	..	4—	..	..	..	..	..	..	..
Urticales	— 1	2—	..	..	..	— 1	..	..	— 3
Celastrales	..	2—	1—	..	..	— 2	..	..	..
Santalales	— 1	1—	— 2	..	— 1	— 1	— 2	..	— 2
Rhamnales	— 3	2—	— 1	— 1	..	— 2	..	— 1	— 2
Rutales	— 1	..	..	..	..	— 1	..	..	..
Meliales	..	..	..	..	..	..	..	..	— 1
Sapindales	..	1—	1— 3	..	..	— 1	..	— 4	— 1
Umbelliflorae	— 3	1—	— 8	..	— 6	— 2	— 5	— 3	— 5
METACHLAMYDEAE	..	..	..	..	..	..	..	..	..
Ericales	..	12—	1—	..	..	..	..	..	..
Ebenales	..	..	..	..	..	..	..	..	— 4
Myrsinales	..	..	— 1	..	..	..	..	..	..
Loganiales	— 1	2—	..	..	..	..	..	..	..
Apocynales	— 2	2—	— 2	..	..	— 4	..	— 1	— 2
Rubiales	— 6	2—	— 5	..	— 1	— 8	— 4	..	— 7
Asterales	—18	19—	6—35	— 1	1— 9	—19	—37	—21	—63
Gentianales	— 1	..	— 1	..	— 1	..	— 1	..	— 2
Primulales	— 5	..	— 2	..	— 1	..	— 3	..	..
Plantaginales	— 3	..	..	..	..	..	..	..	— 1
Campanales	— 1	1—	— 3	..	..	— 1	..	— 1	..
Polemoniales	— 3	..	— 5	..	— 2	..	— 1	..	— 2
Boraginales	— 4	..	1— 2	..	..	— 4	..	— 2	— 2
Solanales	— 2	1—	1— 5	..	— 9	— 3	— 3	— 3	— 3
Personales	— 2	1—	—10	..	— 4	— 4	— 3	— 5	—10
Lamiales	— 3	..	—10	— 1	— 2	— 3	1—14	— 7	—13
MONOCOTYLE-DONEAE	..	..	..	..	..	..	..	..	..
Pandanales	..	..	..	..	..	..	..	..	— 1
Helobiae	— 1	..	..	..	..	..	..	..	..
Glumiflorae	..	—169	..	..	— 1	..	..	..	..
Spathiflorae	..	..	..	..	..	..	— 1	..	— 4
Farinosae	..	..	..	..	..	..	..	..	— 6
Liliflorae	— 8	— 7	— 4	..	— 8	— 6	—17	..	— 9
Scitamineae	..	..	..	..	..	..	..	..	— 2
Microspermae	..	..	..	..	..	— 1	..	..	— 7

rusts on the latter group are diploid phases of heteroecious species, and all the rusts on the Cupresseae are diploid phases of species of *Gymnosporangium*. Since all the other long-cycled rusts known to occur on these groups are haploid phases of species assigned to the Uredinaceae[13] (Melampsoraceae including *Coleosporium*), it is of special interest to note that autoecious long-cycled forms are unknown in this rust family except in the genus *Melampsora*. This genus includes, besides the species having aecia on Abieteae (*Larix*, *Pinus*, *Abies*, and *Tsuga*), another group of species having aecia on dicotyledons or monocotyledons. Among this latter group the aecia occur on several orders of the dicotyledons, including Rhoeadales (*Chelidonium* and *Corydalis*), Saxifragales (*Saxifraga*), Violales (*Viola*), Euphorbiales (*Mercurialis*), Cunoniales (*Ribes*), and Celastrales (*Euonymus*). All these heteroecious species have their diplonts on Salicales (*Populus* and *Salix*).

The genus *Melampsora* is the only known genus of the Uredinaceae having aecia on gymnosperms which also includes species having aecia on dicotyledons and monocotyledons. As noted previously, it is also the only genus of this rust family including autoecious species. These autoecious species occur on various orders of the dicotyledons, including Saxifragales (*Saxifraga*), Geraniales (*Linum*), Thymelaeales (*Wikstroemia*), Bixales (*Idesia*), Passiflorales (*Passiflora*), Guttiferales (*Hypericum*), Euphorbiales (*Euphorbia*, etc.), Salicales (*Salix*), Apocynales (*Apocynum*, *Cynechium*), and Personales (*Pedicularis*). It would appear that the wide distribution of the aecial hosts for the various species of *Melampsora* is correlated with the occurrence of aut-eu-forms in the genus. The genus *Olivia*, classified by Arthur in the Uredinaceae, also includes at least one autoecious species. It may be questioned, however, whether this genus is properly assigned to that family. Dietel (1928) includes it in the Pucciniaceae.

In the Aecidiaceae (Pucciniaceae) autoecious species are the rule in the subfamilies Raveneliatae, Uropyxidatae, and Phragmidiatae, and they occur commonly in the Dicaeomatae. If *Tranzschelia* may be interpreted as a primitive form related to the Raveneliatae, then heteroecism occurs only in the more primitive members of this group.

The genus *Nyssopsora* is also of interest in this connection. While Arthur classifies this genus in the Phragmidiatae, Dietel (1928) would include it along with *Triphragmiopsis* in the Raveneliatae. *Nyssopsora*, according to the interpretation of Tranzschel (1925) and Dietel (1928),

[13] Except for the inclusion of *Coleosporium* in the Melampsoraceae, the nomenclature of rust families and subfamilies follows that used by Arthur in the North American Flora.

includes two groups of species—several microcyclic forms on Umbelliflorae, and two hemi-forms, *N. Cedrelae* (Hori) Tranz. and *N. Koelreuteriae* (Syd.) Tranz., on Meliaceae and Sapindaceae. Tranzschel (1925) has suggested that these hemi-forms, because of the resemblance of the teliospores to those of the micro-forms on Umbelliflorae, are heteroecious with aecia on Umbelliflorae. If Tranzschel's suggestion proves true, we would have additional evidence that the primitive members of the Raveneliatae were heteroecious. The rusts classified in the Uropyxidatae and Phragmidiatae are all autoecious so far as known.

Heteroecism is the rule in the Aecidiatae (*Gymnosporangium* and *Gymnotelium*), which may be interpreted as a special isolated group that has given rise to no other forms. With the exception of the Aecidiatae, just noted, heteroecism is most common among the Aecidiaceae, in the subfamily Dicaeomatae. This group is presumably the most primitive and and the one from which the other subfamilies (with the possible exception of the Aecidiatae) have arisen.

As has been shown in the preceding discussion, the heteroecious rusts predominate on the more primitive families of angiosperms. Autoecious eu-forms are most common on the members of the Metachlamydeae and on the more modern or at least more advanced members of the Archichlamydeae (Polypetaleae and Apetaleae), such as the Euphorbiales, Rosales, Leguminosae, and Umbelliflorae. In North America eighty-three per cent of all the aut-eu-forms occur on the above-mentioned orders. If brachy-forms are included the figure is eighty-seven per cent.

Autoecious rusts, then, are most abundant on the families of hosts which have gone through the greatest amount of evolutionary development. Since rusts have clearly evolved more or less along with their hosts (Dietel, 1904), the distribution of autoecious rusts as outlined above would appear to support the view that they are more modern than the heteroecious rusts.

The evidence brought forward in the discussion of the origin of the various types of life cycle has tended to show that, except for the brachy-forms, the great majority of the rusts of reduced life cycle may be derived from heter-eu-forms. This conclusion, together with the evidence just presented with reference to the predominance of heteroecious forms on the more primitive angiosperms as well as on gymnosperms and pteridophytes, and the occurrence of the great majority of autoecious rusts on the more modern families of angiosperms, leads to the suggestion that heteroecism may not merely be one of the ancient characters in the rusts

but that the ancestral forms of our present-day rusts were probably all heteroecious.

This conclusion is quite in line with the suggestion of Blackman (1904), who says:

> As the heteroecious forms are confined to those possessing the aecidium, i. e., to the more primitive it seems probable that heteroecism may not be, as generally conceived, a later adaptation, but may actually be the primitive condition in the group. Although we are ignorant of the origin of the group it is possible to conceive that the sporophyte was first developed in connection with life on another host, just as the sporophyte in the higher plants seems to have been developed in connection with a new terrestrial existence. The autoecious eu-forms would then be the first step in reduction—a purely environmental one; later a morphological reduction of the number of spore-forms would appear to have taken place.

Most of the writers who have discussed the origin of heteroecism, including Fischer (1898), Klebahn (1904), Christman (1907a), McAlpine (1906), Olive (1911b), Grove (1913b), and more recently Mordvilko (1926), have derived heteroecious from autoecious species in various ways. Their individual opinions are well summarized by Orton (1927), who argues for the primitive nature of heteroecism. Arthur (1924, 1929) also holds the view that the primitive rusts were heteroecious and pleomorphic.

THE ORIGIN OF AUT-EU-FORMS

Since the discussion which has been presented in the preceding pages has led to the conclusion that heteroecism is primitive and the original condition in the immediate ancestors of existing rust species, it becomes desirable to inquire further into some of the relations between heteroecious and autoecious forms and to determine whether it is possible to derive the autoecious from the heteroecious forms in any acceptable manner.

Examples of the occurence of an aut-eu-form on the aecial host for a correlated heter-eu-form have been frequently cited as supporting evidence by those (Olive, 1911; Grove, 1913b; Mordvilko, 1926) who have concluded that a progressive development has occurred from short-cycled forms through autoecious to heteroecious forms. Clear-cut correlations of this sort, however, are not numerous, and where they occur an -opsis form is usually present in the series and a micro-form exists in all cases (see table 10 p. 93). In the opinion of the writer the accumulated evidence that micro-forms are derived and reduced types is too clear to admit of their being primitive. The view might still be held, however, that they have arisen by reduction from the autoecious rather than from the heteroecious forms in such series. The chief objection to such a view-

point is that the occurrence of cases of an autoecious rust on the aecial host for a similar heteroecious species is very rare, while it is common to find that all the rusts on members of certain host families are heteroecious or derived micro- and -opsis forms. Taking into consideration, for the sake of simplicity, only rusts belonging to *Puccinia* and *Uromyces* (excluding species of tropical and subtropical unconnected *Uredo*), the following families may be cited, among others, to which this statement applies: Ranunculaceae (except on the genus *Caltha*), Berberidaceae, Aristolochiaceae, Papaveraceae, Fumariaceae, Loasaceae, Capparidaceae, Cruciferae, Polygalaceae, Crassulaceae, Saxifragaceae (excepting the genus *Montinia*), Portulacaceae, Malvaceae, Grossulariacae, Urticaceae, Sapindaceae, Caprifoliaceae, Adoxaceae, Carduaceae-tribe Astereae only (except the rusts on *Baccharis*), and Scrophulariaceae.

If the autoecious rusts are primitive and the micro-forms are derived from them, there should be a considerable number of autoecious rusts on the aecial hosts of heter-eu-forms showing correlation with micro-forms. As previously noted, such cases are rare. In a large number of cases in which aut-eu-forms occur they are not correlated with the heter-eu- or the micro-forms occurring on related hosts, this fact indicating that they belong to another group of species. In several cases, notably in the Polygonaceae and the Caryophyllaceae, the majority of the autoecious rusts are species of *Uromyces*.

The argument has been presented in the preceding pages that the aeciospores of a heteroecious rust cannot be expected to attack the aecial host unless an endo-condition intervenes (as in *Endophyllum*, the -opsis forms with repeating aecia, and endo-*Peridermium*). If the possibility is admitted of the origin of autoecious eu-forms from heteroecious forms by the simple expedient of the aeciospores attacking the aecial host, then it would appear that such autoecious forms should be more numerous. We should expect to find aut-eu-forms of *Coleosporium*, *Melampsora*, *Pucciniastrum*, *Cronartium*, etc., developing on the Abieteae, and yet no such forms exist.

Is it possible, then, to derive autoecious from heteroecious rusts in any logical manner on the basis of present evidence? Attention has been directed in a number of places in the preceding pages to the presence of urediniospores in the telia of micro-forms which are clearly correlated with heteroecious rusts. One such species is *Uromyces Ficariae*. In this species it has been pointed out that these urediniospores are remarkably like those of the correlated heter-eu-form *U. Rumicis*. In such a case the diploid conidial spore appears on the aecial host. Being merely a conidial

disseminating spore, the objection to its infecting the aecial host is not the same as in aeciospores. To be sure, such spores do not usually infect the aecial host in the heteroecious species. They infect only the host on which they are borne. When, however, they occur in the telia of a micro-form which has become established on the aecial host, they are in a new food relation. It does not seem to the writer too much to imagine that, after numerous generations of the production of urediniospores on the aecial host in association with the micro-form, such urediniospores may acquire the ability to infect the aecial host. The objection may be raised, and rightly so, that one would not expect a true eu-form to develop in such a way from a reduced micro-form which has already lost the ability to produce aecidia. In answer to this objection attention may again be called to the existence of a number of -opsis forms whose relationship is clearly with heter-eu-forms and which belong to the class that has been explained by assuming that they represent transitional conditions developed in the origin of a micro-form from a heter-eu-form. In such forms both aecia and telia are retained and occur on the aecial host. If urediniospores should appear in the telia of such a transitional form and should ultimately acquire the ability to infect the host on which they were borne, we should have every condition for the development of an aut-eu-form indirectly from the heter-eu-form. That -opsis forms, whose relationship is with heter-eu-forms, exist in which urediniospores are occasionally developed is well known. Among such may be mentioned *Uromyces Aconiti-Lycoctoni* (DC.) Wint. and *Puccinia Calochorti* Peck.

If this reasoning be applied to the species listed in table 10, it will be noted in the first group that there exists *P. Epilobii-Fleischeri*, an -opsis form on *Epilobium* having aecial and telial characters similar to those of *P. Veratri*. Should urediniospores appear in such a transitional -opsis form, it might conceivably give rise on the one hand to the aut-eu-form *P. Epilobii-tetragoni* which has the systemic aecial character of *P. Veratri* as well as similar teliospores, and on the other hand to the micro-form *P. Epilobii* which develops in a systemic manner similarly to the haplonts of all the three forms of longer cycle.

Similarly, through *Tranzschelia tucsonensis*, an -opsis form occurring on *Anemone tuberosa* having the aecial and telial characters of *Tranzschelia punctata*— a heter-eu-form with aecia on *Anemone*, *T. cohaesa*, an eut-eu-form on *Anemone*, may be derived as well as the micro-form *T. fusca*.

In the group having aecia on *Euphorbia*, several heteroecious forms, several aut-eu-forms, and several micro-forms are involved. In the group occurring on *Adoxa* the -opsis form is missing. In deriving autoecious

TABLE 10

Correlation between heter-eu- and aut-eu-forms

HETER-EU-FORMS	-OPSIS FORMS	MICRO-FORMS	AUT-EU-FORMS
Puccinia Veratri I on *Epilobium* II, III on *Veratrum*	P. Epilobii-Fleischeri I, III on *Epilobium*	P. Epilobii III on *Epilobium*	P. Epilobii-tetragoni I, II, III on *Epilobium*
Puccinia Nolitangeris I on *Adoxa* II, III on *Impatiens*		P. Adoxae III on *Adoxa*	P. albescens I, II, III on *Adoxa*
Uromyces Pisi, etc. I on *Euphorbia* II, III on Fabaceae	U. excavatus I, III on *Euphorbia*	U. striatus etc. III on *Euphorbia*	U. proëminens I, II, III on *Euphorbia*
Tranzschelia punctata I on *Anemone* II, III on Amygdalaceae	T. tucsonensis I, III on *Anemone*	T. fusca III on *Anemone*	T. cohaesa I, II, III on *Anemone*

rusts in this manner it is to be expected that the transitional -opsis form would in many cases disappear.

This method of deriving the autoecious rusts may be unnecessarily involved. It may be that in rare instances the aeciospores have acquired the ability to infect the host on which they were borne without assuming an endo-condition, and have thus given rise to urediniospores. It is

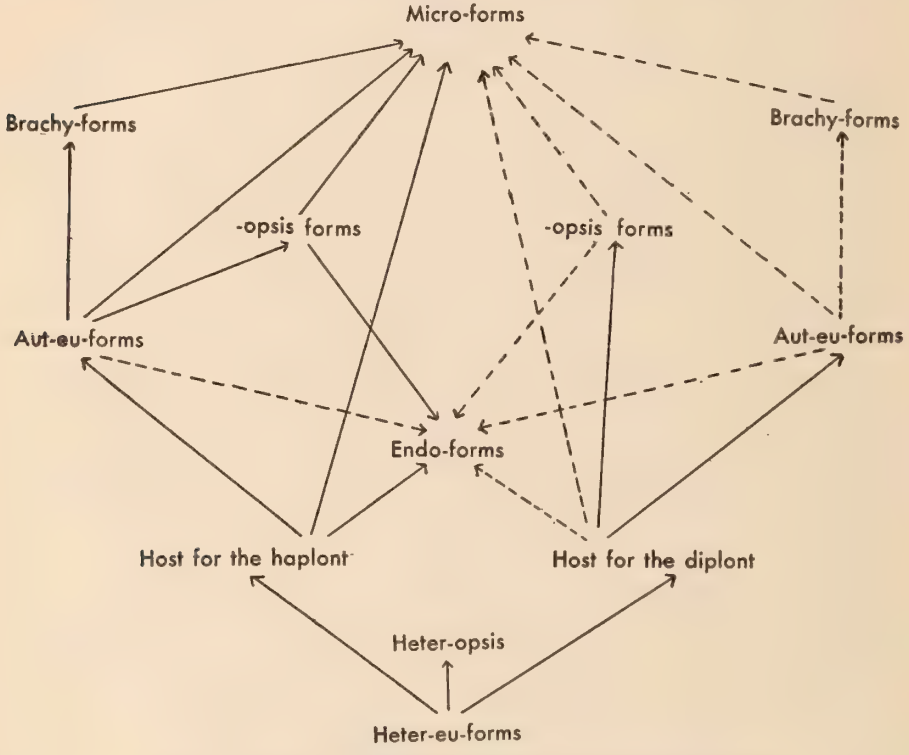

Fig. 1. Diagram illustrating the interrelations and origin of the various types of life cycle in the rusts.

possible that autoecious species may have arisen on the host for the haploid phase in this simple manner.

It is customary also to assume that the basidiospore is incapable of infecting the host which bears the diplont of a heteroecious species. All culture work has supported this assumption, and certainly in general this is true. If heteroecism is primitive, however, it is possible to account for certain autoecious species which occur on the host for the diplont only by assuming that rarely the basidiospores have acquired the ability to infect the host which bore them, thus establishing the haploid thallus on the

host for the diplont. It is only by this method that it is possible to account for the origin of the aut-eu-*Melampsora Amygdalinae* Kleb. on *Salix*; the aut-opsis *Gymnosporangium bermudianum* (Farl.) Earle on *Juniperus;* the aut-opsis *Coleosporium, Synomyces Reichei* (Diet.) Arth. on *Stevia;* the aut-eu-*Puccinia Komarovi* Tranz. on *Impatiens;* and the group of autoecious *Stipa* rusts mentioned on page 49. From autoecious species derived in this way on the host for diplont, a regressive development through -opsis and brachy-forms to micro-forms might also take place.

The method of deriving autoecious from heteroecious rusts by the two methods suggested above, together with the relationship and origin of the various types of life cycle, may be illustrated diagramatically as shown in figure 1 (p. 94). In this diagram the solid lines serve to indicate probable methods of origin, examples of which have been cited in this paper. Broken lines indicate possible methods of origin for which no specific examples are known. It seems probable that the greater development has taken place through transfer to the host for the haplont.

It would appear to the writer that the derivation of autoecious from heteroecious rusts in some such manner as has been outlined offers no greater difficulty than the derivation of the heteroecious from autoecious species, and that the former method obviates the necessity of explaining away the mass of evidence that heteroecism is more primitive.

TAXONOMIC CONSIDERATIONS

The close interrelations of the species of rusts on related hosts as brought out in the discussion of the origin of life cycles has a very important bearing on generic nomenclature in the group. Reference has previously been made (p. 28) to the type of correlation existing between species of *Uromyces* and *Puccinia* of similar life history. It will be recalled that a considerable number of pairs of species are known in these genera which have the same life history, occur on identical or closely related hosts, and are alike morphologically in all spore forms with the exception that one develops one-celled and the other two-celled teliospores. It is clearly evident that the species of such a pair are closely related, quite certainly derived one from the other, and more closely realted to each other than to any other species of either genus. In view of this situation it is questionable whether it is possible to justify the maintenance of the genera *Puccinia* and *Uromyces* separately. *Uromyces* is presumably derived from *Puccinia*. There is considerable evidence to indicate that the two-celled teliospore is the ancestral type in the Aecidiaceae. These genera should perhaps be united. It has been suggested by Arthur and

Fromme (1920, pp. 281, 285, 291, etc.) that correlated species of *Uromyces* and *Puccinia* of the type mentioned should be united under one name. Such a procedure, however, would not seem to be fully justified. All the evidence available points to the conclusion that such correlated species are physiologically distinct as well as differing in the morphological character of the number of cells in the teliospores. They should be retained as separate species or varieties except, perhaps, where teliospores of both types are found mixed in a single sorus.

The correlation between rusts with different life cycles occurring on closely related or identical hosts, which has been mentioned at various points in the preceding discussion, strongly suggests that their real relationship is best expressed by considering them physiologic races of the same species. Usage and convenience, however, make it desirable that they be treated as separate species. Certainly correlated forms of diverse life history are more closely related phylogenetically to each other than they are to any of the species of similar life history occurring on other host families. The immediate relationship of such correlated forms offers one of the strongest arguments against using the type of life cycle as a basis for generic classification, since under such a system these closely related species are placed in different genera. Most students of the taxonomy of rusts are now agreed that life cycle should not alone be made the basis of generic classification, and hence micro-, -opsis, and brachy-forms of *Uromyces* and *Puccinia* are commonly treated along with the eu-forms.

In other cases, particularly among the micro-cyclic forms, much inconsistency is manifest in the taxonomic literature. In cases in which close correlation is evident, particularly in micro-telial forms such as *Necium Farlowii* and *Gallowaya pinicola*, the problem is not a difficult one, and most writers would now place these genera (both mono-typic) with *Melampsora* and *Coleosporium* respectively. In the cases of *Ameris* and *Teloconia*, the micro-cyclic forms on *Rosa* related to *Phragmidium*, the former of which has one-celled and the latter two-celled teliospores, the problem is more difficult. Should the species of *Ameris* and *Teloconia* be included in *Phragmidium*? Certainly to leave them in *Uromyces* and *Puccinia* is inconsistent, since their relationship is clearly with the Phragmidiatae.

The real problem, however, is with the endo-forms. In the case of the monotypic genus *Kunkelia* there would seem to be little objection to combining this with *Gymnoconia*. Certainly to include it with the form genus *Cacoma* is not a logical procedure. The question might be raised as to the real relationship of *Gymnoconia*. It is entirely possible that this is really an

-opsis *Phragmidium* which in the process of simplification has reverted to the original two-celled teliospore type as did *Teloconia*. Perhaps, however, both *Gymnoconia* and *Teloconia* are best interpreted as survivals in a regressive development from the ancestral type of *Phragmidium*.

If the interpretation of the endo-Peridermiums which has been offered is the correct one, are these repeating forms to be left in the form genus *Peridermium*, transferred to *Cronartium*, or must a new genus be erected to accommodate them?

If the species of *Endophyllum* represent merely a special type of life cycle in *Puccinia* and *Uromyces*, how can we classify them to show their immediate relationships? To combine *Uromyces* with *Puccinia* as suggested previously would greatly simplify the problem of the disposition of *Endophyllum*. The only workable method of classifying species in the rusts particularly in large genera like *Puccinia*, is to arrange them according to the relationship of their hosts. In the cases of heteroecious species, however, closer relationships would usually be brought out by arranging them according to the host for the haploid phase instead of for the diploid phase as is now the common practice. It is only by such a method that the real relationships between the heter-eu-forms and correlated endo- and micro-forms could be clearly indicated. For the tropical endo-forms whose relationship cannot at present be traced, the generic name *Endophyllum* could be retained as that of a form genus.

It is my purpose at this time, not to attempt a solution of these nomenclatorial problems, but rather to point out that, if classification in the rusts is to approach a natural system, the relationships as pointed out in the preceding discussions must be given consideration.

THE OCCURRENCE OF PYCNIA IN RUSTS

It would appear from the evidence presented that an inherent tendency to change develops in some species or in some races of certain species. The influence which brings about this tendency has usually been attributed to climatic factors, but it would appear to the writer that it is of a more fundamental nature. It is perhaps true that climatic factors may operate after the tendency to change becomes manifest. Is it possible to obtain any evidence as to what this inherent tendency may be?

In the foregoing discussion of the origin of life cycles an attempt has been made to bring out as accurately as possible the known facts with reference to the occurrence or abscence of pycnia (spermagonia). Pycnia always develop on the haploid thallus and are hence composed of uninucleate cells, and the pycniospores are uninucleate. It may be stated as the

general rule, not, however, without exception, that pycnia are present in eu-forms whether heteroecious or autoecious except in those which furnish some evidence of being in an unstable condition as to life history (as in *Puccinia insperata*, *Uromyces Rikerianus*, etc.). They are present in most typical -opsis forms possessing ordinary discontinuous generations (as *Puccinia claytoniata*). They are likely to be absent or sporadic in appearance in those -opsis forms which seem to be transitional in character. They are present in most true brachy-forms, but may be omitted (as in *Trachyspora Alchemillae*). They are absent in the great majority of micro-forms. They seem to be known in most species of *Endophyllum*, though apparently sporadic in appearance and generally absent in those forms which are uninucleate throughout. They are absent, as would be expected, in micro-forms which have predominantly binucleate mycelia. They may be absent in micro-forms (as *Puccinia Malvacearum*) which present the usual type of nuclear history. No pycnia have been recorded for *Necium Farlowii*, *Chrysomyxa Abietis*, or *Ameris rosicola*. Even when recorded for a given species their development is often erratic, and many collections do not show them or they may be abortive as in *Gallowaya pinicola*. In *Puccinia Grindeliae*, *P. Cryptotaeniae*, and others, they occur rarely and in the first-named species only on certain hosts.

In connection with his studies of heterothallism in the rusts, Craigie (1927a) has shown that pycnia occur on both + and − mycelia in heterothallic species. Craigie (1927b) has also presented evidence to show that pycniospores exercise the function of supplying the opposite 'sex' element to mycelia from monosporidial infection in heterothallic species. The mycelium from a monosporidial infection in such species always produces pycnia but ordinarily no aecidia develop. If, however, pycniospores from a mycelium of opposite 'sex' are mixed with the nectar of the pycnia in the monosporidial infection, aecia soon develop.[14] Just how the pycniospores function to bring about this result has not yet been demonstrated.

For our present purpose the important consideration is that the pycnia are quite constantly associated with long-cycled species and that they are omitted most commonly in those which give some evidence of being in an unstable condition as to life history and in short-cycled species or those of

[14] It is possible that Olive (1911b, p.143) was describing a monosporidial infection of a heterothallic species when he wrote: ". . . . the sexual fusions undoubtedly impart the stimulus necessary for aecidiospore production. A case in point was observed in my preparations in which in certain old sterile aecidium cups no fusions had apparently taken place and consequently no spores had been formed. The uninucleated cells of the sorus appeared, however, to be able to continue growth for some time: but the resulting pustule did not in any case sufficiently develop to break through the epidermis."

reduced life cycle. If the pycniospores exercise the function indicated by Craigie's work, then it would appear quite probable that they would be functionless in homothallic species and might soon be dropped from the life cycle. It also seems probable that when they are absent the species is homothallic. Preliminary culture experiments conducted by the writer with *Puccinia Malvacearum*, a micro-form which does not develop pycnia, strongly indicate that in this species every infection, monosporidial or otherwise, develops one or more sori of teliospores. The indications are that this species is homothallic.

Is it possible that the 'inherent tendency' to a change, to which reference has previously been made, and which apparently results in a shortening of the life cycle, is associated with the loss of heterothallism? It is perhaps an unwarranted procedure to base much speculation on the results of Craigie's work, since he studied only two species of eu-forms, one heteroecious and the other autoecious (*Puccina graminis* Pers. and *P. Helianthi* Schw.), and has not yet shown just how the pycniospores function. However, the fact that pycnia are so universally present in normal heter- and aut-eu-forms suggests that heterothallism may be a primitive character in the rusts and the usual condition in the present long-cycled species. With the loss of heterothallism and the development of a homothallic tendency, the pycnia would no longer be essential structures, and with the loss of function it might be expected that they would be dropped. On the other hand, their function, as indicated by Craigie's work, is of such a special nature, and in ancestral or primitive rusts doubtless was so much more closely related to true 'sexuality' than in the present-day rusts, that it is not surprising that pycnia show a tendency to persist for a long time even in rusts which must be homothallic (as in the uninucleate race of *Kunkelia nitens* which develops pycnia).

The development of homothallism and the loss of function of the pycniospores may bring about an influence which results in many cases in a tendency to change, leading toward a simplification in life history, with which is often associated a simplification in the nuclear history which may occur in various ways, as has been shown in the micro- and endo-forms.

While it is noticeable, as brought out in the preceding discussion, that pycnia are lacking or are sporadic in development in many species which exhibit a composite life cycle, and while the suggestion made in the preceding paragraph may be valid for certain species, it must be admitted that a shortening in life cycle probably occurs in many cases without the loss of heterothallism. As previously voted, pycnia occur in most brachy-

forms and in many true -opsis forms and are retained in a few micro-cyclic species.

It is perhaps idle to speculate on this subject in the absence of more complete information. Studies must be made on a wide range of species and genera, including some of those which have been mentioned in this paper, before we shall have a reasonable basis for discussion. Certainly Craigie's results open the way for a vast amount of work which will have a fundamental bearing on the subjects discussed in this paper.

SUMMARY

A composite summary of the hypotheses which have been stated at various points in this paper and which would seem to be supported by the discussions which have been presented, may now be stated as follows: The ancestral rusts, like the older species in existence to-day, were heteroecious, heterothallic, and pleomorphic. The autoecious long-cycled rusts have developed from heteroecious species, in general without the loss of heterothallism, in two distinct ways: some, probably the great majority, have arisen by a transfer of the full life cycle to the aecial host of the parent heter-eu-form, and some by a similar transfer to the host of the diploid phase. The brachy-forms have all been derived from autoecious species, as have also some of the -opsis and micro-forms. The great majority of the -opsis and micro-forms, together with nearly all the endo-forms, have been derived from the haploid phase of heteroecious rusts. Reduction in life cycle has in many cases been accompanied by the development of homothallism. The present general trend of development would appear to be toward the micro- and endo-forms.

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